1. On the Carpus and Tarsus of the Anura.

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I. INTRODUCTION.

a. *General.*—While, during the last few years, the researches of

Wiedersheim and his pupil Kehrer, and of Baur (1), have added considerably to our knowledge of the limb-skeleton of the Urodela, that of the Anura has received much less attention. The most important investigations recorded since the classic of Gegenbaur (18), are those of Born (3, 5). Brühl has published (11) figures of a somewhat extraordinary character, pertaining to some seven or eight genera; but concerning these we have little to say, except that we fully endorse Born's criticisms and corrections of them (6, pp. 48 *et seq.*).

Born's latest communication purports to be somewhat revolutionary, so far at least as the carpus is concerned (6, p. 62). It will be seen, however, in the sequel, that we are unable to accept his determinations; and as the discovery of new elements and relationships has led us to differ from most of our predecessors, in our estimate of the morphological value of leading elements of both carpus and tarsus, it is binding upon us to preface this paper with an account of those observations upon which our dissensions are based. In accordance, then, with the exigencies of the case, we shall divide the paper into two sections: viz.:—firstly, a *general part*, in which will be given a review of the morphology of the carpal and tarsal elements, together with a detailed account of those hitherto unrecognized structures, whose discovery has necessitated a redetermination of the value of any one or more constituents; and, secondly, a *special part*, in which the leading families will be taken successively, the characters of the carpus and tarsus of each being noted in the light of the preceding section, and special peculiarities dealt with.

b. *Nomenclature.*—Our investigations do not profess to be exhaustive; they leave much to be settled, and we have accordingly refrained from introducing a nomenclature which might embody a premature expression of homological relationships with the limbs of other animals. In dealing with elements whose morphological value remains in the least degree doubtful, we have, for these reasons, adopted the nomenclature of Ecker (17) as being the more empirical and better suited to our purpose than the alternative one of Dugès (16).

In describing the pre-hallux (calcar), we have, in order to facilitate comparison with the works of our predecessors, adopted the older system of nomenclature, calling the outermost digit the fifth, the innermost one the pre-hallux or calcar, and that next to it the hallux or first digit.

New terms have been introduced only where unavoidable; and some of these are, for reasons already given, purely empirical.

c. *Material.*—It will be seen, from the second part of the paper, that we have examined the limbs of 37 genera and 60 species—adequate representatives of all the leading families as defined by Boulenger (7), with the exception of the *Dyscophidæ, Dendrophryniscidæ, Amphignathodontidæ,* and *Hemiphractidæ.* For these specimens our grateful acknowledgments are due mainly to Prof. Huxley, and to Mr. G. A. Boulenger of the Natural History Museum. To the last-named gentleman we are indebted for further aid and advice always most cheerfully given; while we have to tender thanks to Prof. W. K. Parker for useful specimens, to Prof. Wiedersheim of Freiburg for the limbs and a larva of *Pipa*, to Prof. W. N. Parker for some exquisitely preserved tadpoles of the Common Frog, and to Dr. G. Baur, of New Haven, Conn., for suggestions and advice.

Some of our best results have been obtained from feet in which ossification was just commencing (ex. fig. 5). At this stage the outlines of the cartilages are more clearly defined than at the earlier ones (*cf.* fig. 9), while there is a total absence of any distortion or displacement consequent upon complete ossification (*cf.* figs. 5 & 6). Identification of this stage by external appearances is very difficult; absolute size, moreover, gives no clue to it, for while in a *Xenophrys* measuring 27 millim. from mouth to vent (fig. 14) all expectations were realized, in a *Brachycephalus* of 20 millim. ossification was found to be complete.

d. *Methods.*—We early discarded the section-cutting method employed by Born (3, 6), chiefly because the results finally arrived at were less satisfactory than those obtainable from clarified preparations. Clarification in potash solution (kindly suggested to us by Prof. Wiedersheim) was tried, but relinquished, chiefly on account of the difficulties experienced in mounting the preparations. Better results were arrived at by clarifying in a mixture of glycerine and potash, and mounting permanently in glycerine jelly; but our best results were all obtained by the use of clove oil, which offers additional advantages in allowing the preparations to be stained. Borax-carmine solution proved most serviceable as a dye; less successful preparations were, however, obtained with picro-carmine, hæmatoxylin, and bismarck-brown.

Our method of procedure was generally as follows:—The limb having been carefully skinned, the larger muscles were dissected off, in order to facilitate staining. The preparation was next immersed for about ten minutes in borax-carmine, and then transferred to acid alcohol (75 parts alcohol, 3 parts HNO_3, and 22 parts water), in order that superfluous stain might be removed; after dehydration in absolute alcohol, it was allowed to remain in oil of cloves. The final process consisted in carefully picking away the soft parts, little by little, with two pairs of small forceps under a simple microscope, while the preparation was still immersed in a glass trough of clove oil. The smaller preparations were ultimately mounted in Canada balsam.

The above method admits of an examination of all parts in the undisturbed state, and consequently of an accurate determination of the relationships of apposed surfaces, such as is not possible with any other. Moreover, in that ossific centres, lines of fusion, furrows, or outstanding processes are rendered equally obvious, it is manifestly not open to objections which might conceivably arise out of exclusive reliance upon the section-cutter's art.

II. GENERAL PART.

Hind Foot.

a. *Metatarsals and Phalanges.*—Setting the pre-hallux aside, the 1st, 2nd, 3rd, 4th, and 5th digits bear, in most genera (*cf.* foot-note on p. 178) respectively 2, 2, 3, 4, 3, phalanges, the 4th, or outermost digit but oue, being the longest. *Pipa* is alone exceptional, for in it the 3rd exceeds the 4th in length.

b. *Astragalus* (*a.*) *and Calcaneus* (*c.*).—These two elements were already greatly elongated in the youngest specimens in which their presence could be detected. When fully formed, the two bones are generally uniform in length; they are relatively longest in the Tree-Frogs, shortest in *Pelobates*. When of unequal length, the pre-axial bone, or astragalus, is the shorter.

Wiedersheim has shown [1], in *Rana esculenta*, that the arteria interossea perforates the membrane passing between these two bones, dorso-ventrally, to reach the plantar surface of the foot. *Pelodytes* is alone exceptional, among all the genera which we have examined, in the fact that its astragalus and calcaneus have become greatly elongated subsequent to complete fusion (Plate VIII. fig. 12), in a manner strikingly suggestive of the tibia and fibula. The above-named artery, however, remains true to its original relationships, a small foramen (*f.i'.*, fig. 12) being left for its transmission. In this, as in all other genera, neither the astragalus nor calcaneus (however much modified) ever undergo any sort of rotation; they lie side by side, invariably complanate with the tibia and fibula.

Wiedersheim has shown further [2] that in the Urodela (*Ranodon, Salamandrella, Cryptobranchus*) a blood-vessel perforates the tarsal region apparently, at first sight, in the manner of the above-named artery of the Frog. Baur has more recently recorded the same fact for *Necturus* (1, pl. i. figs. 12 & 17). Hyrtl, describing the vascular system of *Cryptobranchus*, says of the crural artery [3]:—"horum ossium biga, cui nulla articulatio intercedit, et quae potius textu fibroso in unum quasi corpus conjungitur, arteriae nostrae commodam praebet occasionem, trajecta syndesmosi intertarsea, *ad dorsalem tarsi regionem emicandi,* quo territorio semel potita, illico in duas, paullo post in quatuor arterias digitales communes dorsales dilabitur, binorum digitorum interstitiis destinatas." There can be little doubt but that this description applies to the vessel noted by Wiedersheim. In that it passes ventro-dorsally, however, it differs *in toto* from that of the Frog, but in this it agrees just as closely with the arteria brachialis of the fore limb of that animal (*cf.* p. 156). These facts tend to show that the perforation in question (*foramen intertarsi,* [auct.]) is probably not homologous with either that of the Urodele hind foot, or that of the fore foot in the Frog itself; if

[1] Anatomie des Frosches, Ecker and Wiedersheim, Part II., Brunswick (1881), p. 86.

[2] "Die ältesten Formen des Carpus und Tarsus d. heutigen Amphibien," Morph. Jahrb. vol. ii. (1876), pp. 421–435.

[3] Cryptobranchus Japonicus, Schediasma anatomicum. Vindobonae, 1865, p. 113.

so, the arteria interossea will not help us in the least in estimating the morphological value of the astragalus and calcaneus.

Wiedersheim asserts (36, p. 211) that in the astragalus we have "ein vereinigtes Tibiale und Intermedium." Gegenbaur (18) and Born, on the other hand, are inclined to regard the tibiale as its sole representative. Proof of the former statement is not forthcoming; and in spite of the most diligent researching, we have been unable to discover, at any stage, the remotest trace of anything at all comparable to a third proximal tarsal. Future research may, perhaps, demonstrate its existence; but, mindful of the elongation of the earliest rudiments of these elements, we incline to the belief that the missing one (? intermedium) has disappeared beyond all recognition, even during the embryonic period.

c. *Tarsalia* 4 *and* 5.—In no Anuran foot hitherto described have there been recognized more than three distal tarsal elements (tarsalia). Examination of the Plates will show that when these remain distinct they are directly associated with the hallux and the two next digits (ex. Plate VII. figs. 8 and 10). The tarsalia of the two outermost digits (4th and 5th) would thus appear to be absent. Gegenbaur first drew attention to the existence, in certain genera, of a ligament (figs. 10, 17, and 19) which passes between the tarsal of the third digit and the head of the fifth metatarsal. He described its relations minutely (18, p. 61), and concluded that "er repräsentirt in ligamentösem Zustande Theile, die unter anderen Verhältnissen als Knorpel gebildet sind." This structure has been recorded in *Hyla*, *Rhinoderma* (Gegenbaur), *Pelobates* (Gegenbaur, 18; Bayer, 2), *Discoglossus* (Wiedersheim, 36, p. 211), and others, and to the list we are able to add (*cf.* Part II.).

Born says of *Phryne* (*Bufo*[1]) *vulgaris* (3, p. 444) "im Bandpolster unter der Basis von Metatarsale IV. traf ich einmal einen deutlichen Rest von Knorpelgewebe, was die Gegenbaur'sche Deutung dieses Bandes als Homologon eines Tarsale IV. durchaus bestätigt." We find that in the adult of *Alytes obstetricans* this ligament (fig. 10) carries a well-marked nodule of cartilage, which lies between the applied heads of the 4th and 5th metatarsals. That this represents one of the missing tarsals is hardly to be doubted from its relationships, but, from its position, it is difficult to say which. Gegenbaur goes on to assert (p. 61), "wenn man das auf ein blosses Ligament reducirte Tarsusstück einem der bei den übrigien Amphibien nachgewiesenen Elementarstücke vergleichen will, so kann man in ihm nur nach Massgabe der Betheiligung des Metatarsus das Tarsale 4 und 5 erkennen, welches bei den Tritonen schon durch ein einziges Stück dargestellt war." In *Bufo*, *Hylodes*, and *Hyla* (Plate VIII. fig. 19) the ligament enters into an extensive connection with the head of the fifth metatarsal, like that originally figured by Gegenbaur (18, pl. 4. fig. 13) for the first-named genus. It fuses (fig. 23) with the postaxial articular border of this bone, and the head of the same is seen to be obviously enlarged as the result of its attachment[2]. It becomes a question of considerable interest, therefore,

[1] See Boulenger (7, p. 303).
[2] Cf. *Xenophrys*, Plate VIII. fig. 17.

whether this enlargement may or may not represent a coalesced 5th tarsal (as, indeed, Gegenbaur was inclined to believe, pp. 64–65). We have failed to detect any trace of segmentation of the cartilage at this point. In the *Hylidæ,* however, a second ligament is present, which passes (fig. 19) from the postaxial wall of the capsule of the tarso-metatarsal joint, upwards and inwards, for attachment to the epiphysial cartilage of the astragalus and calcaneus. This ligament carries at its outer end a wedge-shaped cartilage, and that we at first took to represent the fifth tarsal. Upon reconsideration, however, we are disposed to regard it as an ordinary intra-articular cartilage of none but physiological significance (for further details see p. 168). Reflection upon these facts has led us to the belief that while the ligament which passes between the third tarsal and the head of the 5th metatarsal is the degraded representative of the 4th and 5th tarsalia, the cartilaginous nodule occasionally carried by it is exclusively a vestige of the 4th one. Gegenbaur records the presence of this ligament in *Rana esculenta,* in addition to the other genera named, and we can confirm his statement. In *R. temporaria,* however, we find no trace of it in the adult, and but a feeble one in the larva. This fact, while lending additional support to Gegenbaur's original deduction, shows how completely the vestige is, as it were, disappearing under our eyes.

d. *Tarsalia* 2 *and* 3 (*Os cuboideum*).—We have already stated that three tarsal elements may exist; on the other hand, the outermost two of these may not unfrequently be replaced in a long bone (cuboideum), represented in its typical condition at $^{2\ 3}$ in figs. 17, 24, 27, 29, 31, & 33. It will be observed in all these cases that this structure overlies, more or less completely, the metatarsalia of the 2nd and 3rd digits; comparison of the same with those forms in which the three tarsalia are found (*Bombinator* or *Alytes,* figs. 8 & 10) leaves little doubt but that the bone represents a confluence of the tarsalia of the 2nd and 3rd digits, as asserted by all recent authorities.

In some cases, however, examination of the adult limb would appear to render this questionable. For example: in *Hyla cærulea* (fig. 19), in which two tarsalia are alone present, the larger one is little, if at all, related to the 2nd metatarsal—the head of which is in apposition with the second and smaller element. Comparison of this tarsus with that possessed of the three tarsalia (figs. 8 & 10) renders it hard, indeed, to say which two elements are represented in the Tree-Frog. Born has already experienced this difficulty in dealing (6, p. 443) with the adults of *Phryne vulgaris* and *Bufo variabilis,* and he admits his inability to settle the question, for want of embryological material.

On turning to the larva of *Hyla* (fig. 21), we find that the outer of the two elements has (unlike that of the adult) more than twice the bulk of its fellow, while it agrees in every detail with the cuboideum in its most typical form (cf. *Xenophrys,* fig. 17). Examination of this element side by side with that of the adult limb (fig. 19) shows that its growth is arrested early in development: it shows, further, that the connection between the innermost tarsal (1) and the head of the second digit is purely secondary, and that the first-named is really the tarsal of the hallux, displaced, as it were, in sympathy with its dwarfed neighbour.

Ecker speaks (17, p. 61) of the cuboideum in *Bufo* as consisting of two pieces. We find that in that genus, as in *Leptodactylus*, a similar shortening up of this bone takes place (*cf.* fig. 23); there can be little doubt therefore that Ecker was misled by that, precisely in the manner indicated above.

The cuboideum, then, must be held to represent the confluent tarsalia 2 and 3. We have to record its presence in the *Ranidæ*, *Dendrobatidæ*, *Engystomatidæ*, *Cystignathidæ*, *Bufonidæ*, *Hylidæ*, *Dactylethridæ*, and *Pipa*.

e. *Tarsale* 1 (*Hallux tarsal*) (1).—This element is of very constant occurrence. Its relations in the *Discoglossidæ* are exceptional and, as will be shown below (figs. 8 & 10), interesting; it lies in them under cover of the naviculare (*n'*), interposed between it and the 1st metatarsal. Gegenbaur appears, in dealing with *Bombinator*, to have mistaken the naviculare for the first tarsal (18, pl. 6. fig. 11); but this is not to be wondered at, in consideration of the small size of the latter. It is wanting as a distinct element in old specimens of *Nannophrys* and *Phryniscus*, and we have found that it fuses in both genera with the naviculare. Born has described and figured it accurately in *Rana esculenta*. Concerning *R. temporaria* he says (3, p. 441) that it "immer in Laufe der Ontogenese bis auf unerhebliche Spuren schwindet." Strictly speaking, this is not the case, for we are in possession of old examples in which it had persisted as a distinct element (woodcut, p. 176, fig. C, *I*). We are inclined moreover to believe that instead of undergoing suppression, as Born imagines, it more probably fuses with the naviculare as in the two above-named genera.

f. *Naviculare and Pre-hallux tarsal.*—Ecker regarded the naviculare of these animals as analogous (17, p. 61) with the element so named (centrale) in the tarsi of the higher animals. Gegenbaur, on the other hand, who, as before stated, confused it with the hallux-tarsal, sums up his conclusions in the words (18, p. 67), "ein Centrale fehlt." Born adopts this view; but he differs from Gegenbaur in that he regards the naviculare as the basal segment (tarsale) of the pre-hallux. He writes (3, p. 448), "von diesen [segments of the pre-hallux] liegt der erste in einer Reihe mit den Tarsalknorpeln, welche Metatarsusträger sind, ahmt dieselben in Form und Structur nach und ist von den Autoren auch, wie erwähnt, immerals 'typischer' Tarsalknorpel aufgefasst worden." Born's determination has been adopted by all subsequent writers. It will thus be seen that the two views entertained as to the morphological value of the naviculare are diametrically opposed, and that a settlement of their differences is indispensable to the full determination of the value of the distal preaxial elements. We have already drawn attention to the fact that the naviculare of the *Discoglossidæ* (ex. *Bombinator*, fig. 8, *Alytes*, fig. 10) is wedged in between the first tarsal and the astragalus, being in fact absolutely central and in a position which cannot, by any stretch of imagination, be said to be "in einer Reihe mit den Tarsalknorpeln." It would be more correct to say that the 1st metatarsal, 1st tarsal, and naviculare are here disposed lineally.

Examination of the Plates will show that the relative size of the naviculare is in no way proportionate to that of the pre-hallux, as might be expected were Born's hypothesis tenable (*cf.* figs. 3, 10, 12, & 17); it is rather the reverse. Choice appears to lie between two alternatives: the naviculare has either grown in and displaced the hallux tarsal proximally (as the *Discoglossidæ* would suggest, figs. 8 & 10, in which case the condition of the latter would, in this family, be secondary) or it has undergone a reduction proportionate with an increase in size of the same. Recent observers are agreed as to the lowly position of the *Discoglossidæ*[1], and it therefore becomes a question of first importance as to how far the arrangement just described in them is primary.

In the youngest *Discoglossidæ* examined by us (*cf.* p. 164), no appreciable difference could be detected in the relative proportions of the two elements under consideration as compared with the adult; we have here, then, strong reason for regarding the condition exemplified in them as really primary. The matter, however, presses still more closely. Examination of those forms in which the pre-hallux is regularly segmented (fig. 19), shows that that segment which Born regards as its metatarsal (*ph.* i.) is generally disposed in a line with the naviculare, *n'* (*cf.* figs. 13 & 19). In *Pelodytes*, however (fig. 13), and less conspicuously in *Alytes* (fig. 10) and *Hyla*, the first-named element is intimately connected with the adjacent hallux-tarsal (1) by means of a well-defined ligament, which runs distally to the naviculare. Comparison of this ligament with that previously referred to as the representative of the 4th and 5th tarsalia, leaves little room for doubting, if argument from analogy is worth anything, that Born's metatarsal of the pre-hallux is, in reality, its tarsal. If this be admitted, there can no longer be any doubt of the homology of Ecker's naviculare (*n'*) with the os centrale tarsi.

This determination brings the tarsus of the Anura into closer harmony with that of the other and, especially, the higher Vertebrata than is now generally admitted, while it sets at rest further doubt as to the value of the hallux-tarsal.

Finally, Ecker has shown (17, p. 128) that the tendon of the adductor longus digiti primi muscle (*m.a.l.* of woodcut, fig. C, p. 176) is inserted into the naviculare. We have found this to be invariably the case whether the hallux-tarsal is present or absent. It follows, therefore, that all possible source of confusion between that element and the naviculare is at an end.

g. *Pre-hallux* (*Calcar*).—The skeleton of the pre-hallux was first figured by Rosenhof (32); he described it (*Pelobates*, p. 84) in the words "tandem etiam in sceleto hoc notari meretur singularis quidam

[1] *Cf.* Cope (12, p. 104) and Boulenger (7, p. 444).

spurisque unguis." It has been likened by some anatomists to a single element in the tarsus (ex. entocuneiform, Owen, 31, p. 184); it is, however, unnecessary to recapitulate these comparisons in detail.

All recent writers are agreed as to the variable nature of the pre-hallux, but the range of this has not yet been fully recorded. As will be seen from an examination of our figures, it is very inconstant in size, shape, and detailed characters. For example: in the adult *Xenophrys* (fig. 17), it consists of a single elongated cartilage which ossifies very late in life, whereas in *Hyla* (fig. 19) it attains a much greater development, and is segmented into four pieces. Disparity in size is by no means confined to members of different families, for in *Pelobates*—the type of the family to which *Xenophrys* belongs—the calcar, while consisting of a single piece, attains enormous proportions and ossifies very early [1]. In this burrowing genus the calcar supports the well-known horny blade, by means of which the animal is enabled to shovel up the earth. This being so, its early ossification is distinctly associated with the functional requirements of the case.

Born at first ascribed (3, p. 448) four segments to this structure in *Rana*, *Bufo*, and others. In his later researches, however, he records considerable variation in the same, stating (6, p. 61), "wechselt doch die Stückzahl v. *Rana esculenta*, zwischen zwei und vier, bei *Bufo variabilis*, zwischen drei und fünf." Our figs. 19 & 19 *a* agree very well with his description, while they represent the maximum segmentation into lineally disposed elements observed in any specimen. We have already shown reason for regarding Born's basal pre-hallux segment as the centrale (naviculare), whence it follows that in no known Anuran does the calcar, as defined by us, ever consist of more than four true segments. This maximum number is reached in *Bufo* [2] (?), *Hyla*, *Hylarana*, *Leptodactylus*, *Nototrema*, and *Rana*—representatives, that is to say, of four distinct families.

Incident upon the foregoing there arises the question as to whether the unsegmented condition of the pre-hallux is the more primitive one, or *vice versâ*. If the latter be the case, traces of segmentation ought to be forthcoming in the larvæ of those forms possessed of the single piece. Born accords to *Rana esculenta* a maximum of three pieces. In old Tadpoles of *R. temporaria*, however, we have detected the presence of four distinct segments of hyaline cartilage: the terminal one of these early degenerates and becomes eventually fibrous, and not until then can that fusion of the parts which Born describes [3] take place. The facts recorded by this author alone for *Hyla* and *Bufo* (*Phryne*) (6, pl. 1. figs. 2 & 3) are, in themselves, sufficient to show that the lineally segmented condition is most probably the primitive one.

We are doubtful as to how far the one or two pieces, met with in

[1] Born makes the assertion (6, p. 59) that it here bears originally two phalanges: this we cannot confirm.

[2] Born (6, p. 61). We have not observed it.

[3] p. 56. We have not observed this.

adults of certain species, may or may not arise by confluence or suppression of individual segments (*cf.* fig. 8); future research must decide this question.

There remain two most important questions. 1, If the segmented condition be the more primitive, may not the whole pre-hallux represent a shortened-up digit? and 2, May not this supposed sixth digit represent a lost ray of the ichthyopterygium?

In *Nannophrys*, *Phyllomedusa* (fig. 19 *a*), *Rhombophryne*, and especially in some species of *Hyla*, the pre-hallux has quite a digitiform aspect, comparing, at first sight, very favourably with the reduced pollex of the fore limb, the homology of which with the other digits nobody disputes (*cf.* Plate VIII. figs. 19 *a* & 20).

That the pre-hallux may, in a sense, resemble the pollex is clear from the preceding; but it must not be forgotten that this resemblance is most marked in the specialized Tree-Frogs. Its segments[1] are, in the embryo, more digitiform than in the adult; and taking all facts into consideration, we incline to a belief in a preponderance of the resemblances over the differences between this structure and a normal digit.

The second difficulty is not easily to be met. That the pre-hallux takes on certain of the essential relationships of a digit is beyond dispute. That it really represents one is another question.

The tarsal of the pre-hallux is, in most cases, in definite articulation with the head of the naviculare (cf. *Pelodytes*, fig. 13). In many forms its second segment is the largest (ex. fig. 27); when this is the case, that may be disposed parallel with the metatarsals, in a manner strikingly suggestive of a serial homology (cf. *Xenopus*, fig. 3, and *Pseudis*, fig. 27). In *Xenophrys*, *Hyla* (figs. 17 and 19), and other genera, this supposed metatarsal sends forwards (backwards *in situ*) a small retral lobe (*); in *Ceratophrys* (fig. 24) this attains a considerable development, and in individuals of this genus it may exceed in size the body of the segment from which it takes its origin.

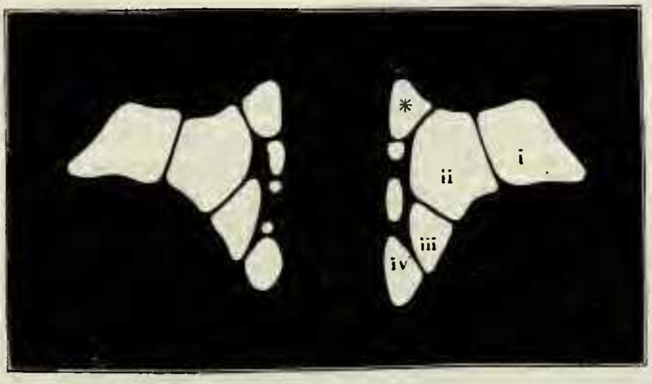
Meckel (29) and Cuvier (15) held, and Born (3), Kehrer (24), and others still hold the pre-hallux to be a sixth digit. Leydig (25), attacking it from a totally different standpoint, argues to the contrary. Gegenbaur at first took a similar view, holding (18) it to be a secondary structure peculiar to the Anura, and his words are echoed by Hofmann (21); subsequently however to the publication of Born's paper, Gegenbaur accepted that author's position, confessing to the same in his well-known text-book. Finally, Born asserts, in his latest paper (6, p. 61) "Übrigens bin ich jetzt geneigt in der starken Variabilität der Gebilde der sechsten Zehe . . . nicht bloss mehr eine Eigenthümlichkeit zu sehen, die derselbem als rudimentärem Organ anhaftet, sondern ich sehe in der häufigen Verschmelzung ein Bestreben ein immer festeres Skelettstück als

[1] Van Deen records (34) an instance in which, in *Rana esculenta*, these lay in a line with the hallux and supported the web. His specimen was, unfortunately, a monstrous one, with four hind legs.

Unterlage für den Fersenhöcker, der vielfach als Grab-Instrument benutzt wird, zu gewinnen."

We have already called attention (p. 150) to the development of a retral process from that which we regard as the hallux-metatarsal. In *Hyla lichenata* this is completely segmented off (* in woodcut, fig. A), forming one of a series of marginal elements,

Fig. A.



The pre-hallux of opposite sides in *Hyla lichenata*. Dorsal aspect. × 6.

which skirt the outer face of the calcar and are, moreover, roughly symmetrical on opposite sides. Comparison of this figure with that of the more normal pre-hallux of *H. cærulea* (Plate VIII. fig. 19) renders it tolerably certain that these nodules are dismemberments of the main mass.

It would be superfluous here to recapitulate the well-known speculations and discussions which turn on the supposed ancestral condition of the pentadactyle limb [1]; it is more pertinent to point out that the evidence against the supposition that all living Amphibia and Amniota have directly inherited a pentadactyle member, is, to no inconsiderable extent, based upon the discovery of fragmentary cartilages in no way indistinguishable from these now under consideration. Such fragments have been discovered flanking both pre- and postaxial borders of the one member or the other in even Man himself [2]; and in the fertile imaginations of Bardeleben, Kehrer (24), and others, we find them exalted to the dignity of lost rays. The last-named author writes (p. 14) "so hätten wir also bei der Beurtheilung des Hand- und Fuss-skeletes der Wirbelthiere künftighin nicht mehr von einer pentadactylen, sondern von einer heptadactylen Urform auszugehen, und von diesem Gesichtspunkte aus

[1] For details and *résumé* see Gegenbaur (19), and Wiedersheim (36), pp. 204–207 and 229–230; also "Zur Urgesch. d. Gliedmassen d. Wirbelth," 'Humboldt,' vol. 5, 1886.

[2] Bardeleben, 'Jenaische Zeitschr. für Naturwiss.' Bd. 19, N.F. xii. Supplem.-Heft 3, 1886. *Cf.* Wiedersheim, 'Lehrbuch,' p. 224, and 'Humboldt,' *cit.*

betrachtet, werden auch fürderhin die 'überzähligen' Finger und Zehen . . . . sondern als atavistische Bildungen angesehen werden dürfen."

Baur is, of all later writers, the one who has done most to combat this doctrine. He advances (1, p. 68 *et seq.*) equally good arguments for regarding these so-called supernumerary digits as purely secondary and adaptive structures, laying, at the same time, great stress upon their late appearance, especially in the case of the pre-hallux itself. The advocates of the opposite belief[1] seek shelter under the stronghold of the *Enaliosauria*, but recent investigation at least suggests that the paddles of those beasts were specialized derivatives of pentadactyle predecessors[2].

We trust to have already shown satisfactorily that the naviculare can no longer be regarded as the hallux-tarsal, as Born supposes; and that admitted, it follows that the pre-hallux conforms to the structural requirements of a sixth digit. More than this cannot be said at present, and further speculation would be useless until the connecting link between the cheiropterygium and its piscine predecessor shall have been discovered. For this we look to the palæontologist.

Setting aside further discussion as to the exact significance of the pre-hallux itself, we cannot refrain from regarding that fragmentary dismemberment of its outer free border, above represented, as an additional argument for the views of Leydig and Baur. If the converse one be justifiable, we should have ample ground for pleading the cause of an octodactyle "Urform," and this would be *primâ facie* no advance at all.

There is a growing tendency to attach too much importance to gristly fragments such as those now under consideration, and it is binding on those who may yet deal with these supposed vestiges (especially as manifested in the higher Vertebrata), that they shall determine at the outset, with greater accuracy than has hitherto been done, what precise relationships they bear to the soft parts. If not, the question bids fair to be reduced ere long to the condition of a *reductio ad absurdum*.

Fore Foot.

a. *Metacarpals and Phalanges.*—The pollex of the Anura under-

[1] Parker writes (P. R. S. vol. 42 (1887), p. 57), "I have frequently noticed that aborted parts, like overshadowed plants, are late to appear, and soon wither, or are arrested in their growth."

[2] Baur, "Bemerkungen über Sauropterygia und Ichthyopterygia," Zool. Anzeiger, 1886, pp. 245–252; also "Die Abstammung d. Amnioten Wirbelth.," Biolog. Centralbl. Bd. 7 (1887), pp. 481–493. See also "On the Phylogenetic Arrangement of the Sauropsida," 'Journal of Morphology,' Boston, vol. i. no. 1 (1887), pp. 93–104; the discovery by Gadow and Baur (herein recorded) of supernumerary phalanges in the manus of *Halicore* and *Manatus* is most welcome at this juncture. See also Baur, "Ueber den Ursprung d. Extremitäten der Ichthyopterygia," Bericht u. d. xx. Versammlung des Oberrheinischen Geolog. Vereins, 1887.

goes, as will be shown later, a by no means insignificant range of modification. In no case, however, is it ever segmented into more than three pieces exclusive of its carpal; it thus never bears more than two phalanges. The other four digits bear each, in order of succession from within outwards, 2, 2, 3, 3 phalanges, certain Ranidæ excepted (*cf.* footnote, p. 178).

The inner border of the metacarpal of the second digit becomes, in the males of certain Anura, as is well known in the case of the Common Frog, variously crested or tuberculated in connection with the overlying "thumb-pad" (2′. fig. 6), or for support of the horny clasper as in *Leptodactylus* (** fig. 25). Leydig has recently described these modifications with great accuracy (26), so far as they concern the indigenous European forms.

b. *Distal Carpal Elements* (*Carpalia*).—In the more specialized forms certain of these unite with each other or with adjacent elements (ex. *Hyla*, fig. 20, *Rhombophryne*, fig. 32); and for the present we shall exclude such from consideration, dealing only with those feet in which the elements remain permanently distinct.

All previous writers are agreed that in such forms five carpalia are represented. While we admit that such *may* be the case, we doubt, as the sequel will show, the homology of that element which our predecessors, not excluding Born (6), interpret as the carpal of the 5th digit.

Carpale 2 (*Trapèze* of Dugès; *Trapezoides* of Ecker).—This element ((2) of our figures) is never more than insignificantly displaced. Examination of any one drawing will show that it lies in a line with the head of the 2nd metacarpal (2′); and comparison of *Alytes* tadpole (fig. 9) shows this to be its primitive position.

It is usually of fair size, becoming well ossified. In the *Discoglossidæ* it undergoes a slight reduction (figs. 6 & 7), and this reaches its maximum, amounting to insignificance in the ♂ of *Leptodactylus* (fig. 25). Comparison of this carpus with the adult *Discoglossus* (fig. 6) and the larval *Alytes* (fig. 9) is sufficient to show that this partial atrophy is to no small extent associated with the specialization and enlargement of its metacarpal.

We have found this element to be free in all but *Brachycephalus*, *Pipa*, and *Rhombophryne*.

Carpalia 3 *and* 4.—In certain forms these two elements become confluent, constituting the nucleus of a large bone (3, 4 *k*, figs. 25, 26, 28), called by Ecker (17, p. 53) the "capitato-hamatum." In the *Discoglossidæ*, *Pelobatidæ*, and *Aglossa*, however, carpalia 3 and 4 are distinct. Considering the general affinities of these three families, and that there are combined among them all the lowest terms of structural detail met with in the whole Order, this point of agreement is the more welcome and suggestive.

Examination of the figs. which we append will show that in the two first-named families there is a tendency towards an increase in size of the 4th carpal and consequent displacement of the 3rd one (*cf.* figs. 5, 7, and 18). The two, however, lie, in all, practically in a line with the 3rd and 4th metacarpals—absolutely so in the

Aglossa. The representatives of that family retain then, in this feature of their organization, a more primitive condition than do any other living Anura. Further comment is needless.

Carpale 5.—All writers have, up to the present, regarded the large element marked *k* as the fifth carpal. In the *Discoglossidæ*, *Pelobatidæ*, and in *Xenopus*, this is large and distinct; and seeing that in the last-named genus the head of the 5th metacarpal (5′, fig. 4) is especially excavated to receive it, the above-named determination would appear to be unassailable.

In the two first-named families (*Discoglossidæ* and *Pelobatidæ*) this element has no connection with the metacarpal, for in them there runs, from the postaxial border of the 4th carpal to the epiphysial cartilage of the 5th metacarpal, a ligamentous band (* figs. 5, 7, and 15). This structure courses ventrally to the distal face of the supposed 5th carpal (*k*), excluding that from direct connection with the adjacent metacarpal.

The absolute identity of this band with the ligament in the hind foot, admitted by all to represent the missing tarsalia 4 (? 5), is irrefutable; and, if argument from analogy is to be trusted, this structure may justly be looked upon as a 5th carpal. If so, the older determination falls to the ground, and the element *k* can no longer be regarded as distal. We are in a position to substantiate this, for the ligament in question carries, in *Xenophrys*, a well-defined nodule of hyaline cartilage which ossifies as age advances (5, fig. 16). This ligament is early differentiated, and comparison of the higher forms suggests that it represents something which, in them, has been lost.

We trust thus to have shown that the 5th carpal is practically absent in the Anura as an order, but that a vestige of it exists in the adults of the *Discoglossidæ* and *Pelobatidæ* (in precisely those forms, that is, in which we might have expected to find it), becoming ossified and attaining its most full development, so far as is at present known, in the genus *Xenophrys*.

c. *Carpale* 1 *and Pollex*.—The pollex is, in all known Anura, relatively small and unimportant. It attains its maximum length in certain American Tree-Frogs (*cf.* Cope, 14, and Boulenger, 7, pp. 338, 339), and among the *Cystignathidæ* (*cf.* p. 170); in other forms, again, it is very short. Born says of it in *Bombinator* (6, p. 62), "einmal fehlte sie ganz, ein andermal waren sogar zwei Phalangen vorhanden;" Gegenbaur omits it in his well-known figure of *Bufo* (18, pl. i. fig. 11), while Brocchi denies its existence in *Hemiphractus* (10, p. 16). We strongly doubt the assertion of the first-named author, and we can only attribute it to the fact that he relied exclusively upon microscopical sections. Small the pollex may be, but absent rarely, so far as our experience goes.

In all but some few forms the body of the pollex is in articulation with a proximal cartilage, *po* i. (the "trapezium" of Ecker, 17, p. 53), of somewhat variable character. In its predominant shape, this element may be fitly compared with the bowl of a very thick spoon.

In *Pseudis* tadpole and *Hyla* (figs. 26 & 20), less conspicuously in *Bufo* and others, it is elongated in the manner of a finger-joint. With the exception of Dugès, who first regarded it (16) as a metacarpal, all investigators have looked upon it as the carpal of the pollex. Examination of its detailed relationships and consideration of its embryological condition (*Alytes*, fig. 9, *po.* i.) leave no room for doubting the accuracy of the latter determination.

Assume what form it may, the pollex usually ossifies more early in the males than in the females. In the *Ranidæ*, for example, it remains in the females for a considerable time simple and unossified (woodcut, fig. B, p. 174). This precocious ossification in the male sex is clearly the result of its connection with the well-known "thumb-pad," for it supports that more or less extensively in different genera and species. In some forms there is a great tendency for it to enter into direct connection with the 2nd metacarpal, either by simple apposition or by fusion with the warted crest of the same. In the male *Discoglossus*, however, the reverse is the case, for it there appears (fig. 6) to have undergone an increase in breadth directly proportionate to its diminution in length. Examination of the living animal shows that this change is an accompaniment of one undergone by the "thumb-pad;" for that is, as it were, duplicated, its lesser representative being alone supported by the pollex.

In the youngest individuals examined by us (e. g. *Ranidæ* and *Alytes*) the pollex had the form of one elongated unsegmented cartilage. It ossifies as a single element in all *Ranidæ*, *Bufonidæ*, and *Discoglossidæ* which we have manipulated. On the other hand, the like is true only of certain genera in the *Cystignathidæ*, *Pelobatidæ*, and *Hylidæ*.

In all forms examined by us, not cited above, it had become more or less thoroughly segmented into two or three pieces (*po.* ii. to *po.* iv. of figs.). These, in some of the Tree-Frogs especially, take on the characters of a metacarpal twice as long as broad and two short phalanges. In them and certain other forms it undergoes an elongation at the same time; in yet others the reverse is the case. It must not, however, be imagined that a converse line of modification is here set up, for *Leptodactylus* (fig. 25), *Pelodytes* (fig. 11), *Ceratophrys*, and *Callula* all show that, while shortened up, it is still segmented into distinct joints; and these, moreover, subsequently undergo complete and independent ossification.

When ossification sets in without previous segmentation, it does not spread from one or more definite centres, but it is diffuse and irregular.

In the males of *Rhombophryne* (fig. 32) and *Lymnodynastes* (fig. 28) the pollex is quite calcariform. The characters of the rest of the member are, in both genera, such as to show, beyond doubt, that we have here to deal with extremely specialized forms.

d. *Ulnare* (*Pyramidale*).—Wiedersheim has shown[1] that in *Rana*

[1] 'Anat. d. Frosches,' Abth. ii. p. 79.

esculenta the arteria brachialis sends up a branch, which perforates the carpus ventro-dorsally, for distribution to the integument and parts adjacent. In some forms (ex. *Discoglossus*, figs. 5, 6, *f.i.*) the bones of the proximal row become definitely notched at this point, enclosing that which we would term [1] a *foramen intercarpi* for passage of the artery. Born has demonstrated the same fact for certain Lacertilia (4, pp. 2–3); while Wiedershiem [2], Baur (1, pl. i. fig. 4), and others have done so, less conspicuously, for the Urodela. Examination of the several descriptions and figures shows that the perforation invariably takes place between the postaxial (ulnare) and central (intermedium) elements of the proximal series.

In certain Urodeles a confluence takes place between these skeletal units; and when this is the case the ulnare and intermedium are invariably those which fuse, and in some of these cases the artery in question perforates the confluent mass. Taking this fact into consideration it is clear that the ulnare is the only element which, under all circumstances, can lie postaxially to the blood-vessel. Seeing, moreover, that the artery agrees in all investigated cases in every known detail of distribution, it is obvious that, in it, we have a convenient landmark by which to estimate the morphological value of the proximal carpals. This said, further arguments are unnecessary in order to show that the so called "pyramidale" of Dugès and Ecker is the ulnare, as Gegenbaur showed and as all subsequent writers admit.

e. *Lunatum* (*l.*)—The extraordinary position in which the fore foot of many living Anura is carried has resulted in a rotation of the parts of the same upon the coalesced radius and ulna, of such a nature that the distal extremity of the ulna comes to be directed towards the palmar surface of the fore foot itself. This rotation is most marked in *Dactylethra*, *Hyla*, *Pelobates*, *Pseudis*, and *Rana*; and it is instructive to find that the tadpoles of these genera do not exhibit it. The distortion resulting from it is such, that we often found it impossible (ex. *Pelobates*, fig. 18) to obtain a comprehensive view of the carpus without first disarticulating the radius. The importance of this observation is by no means slight, for there can be little doubt but that we are to seek the clue to the remarkable delineations of some authors, to displacement of these parts, consequent upon their having flattened them out.

From what we have said (*suprà*) concerning the course of the *arteria brachialis*, it will be clear that the lunatum can only represent the radiale or the intermedium—one or both—of the less modified forms. Gegenbaur was unable to make up his mind (18, p. 13) as to whether this bone represents a confluence of these two elements or a persistent radiale—the intermedium having disappeared. He further suggested the possibility that the last-named may have been absorbed by the radius and ulna during coalescence.

Born puts forward, in his latest communication (6, p. 62), the startling supposition that the lunatum is the intermedium. He bases

[1] Uniformly with the *f. intertarsi* of the hind foot (p. 144).
[2] Morph. Jahrb. vol. 2. (1876).

his deduction upon appearances presented to him in sections of two "vierbeinigen Alyteslarven." On p. 158 will be found a full statement of our reasons for refusing to accept the main observation upon which this view it based; consideration thereof will show that even if that be reliable, there are still insufficient grounds for assuming *e vestigio* that the lunatum is the intermedium.

When, to the above, we add that all attempts to discover at any stage, in its proper place, a trace of a third proximal carpal element, have failed us, there is nothing left us but to record our belief that the lunatum represents the radiale alone, and that all traces of the intermedium have vanished from even the ontogenetic record (*cf.* hind foot, p. 145).

f. *Postaxial Centrale* (5th carpal of earlier observers.) (*k*).—We have discussed this element sufficiently under the head of "carpal 5" (p. 154) to render further details needless. It is present as a distinct element only in the lower families; its great size and comparative uniformity are its most striking features. If the morphological value claimed by us (p. 154) for that new element which we interpret as the 5th carpal be accepted, this one, looked at from all possible standpoints, can only represent a centrale. We propose therefore to term it, in accordance with its position, the postaxial centrale, by way of distinction from the element next to be dealt with.

g. *Naviculare* ("scaphoïde" of Dugès) (*n.*).—This element is by far the most troublesome in the whole carpus, if not in carpus and tarsus taken collectively. It may fuse with others in a manner to be described later, but in all the lower representatives of the Order it is permanently distinct. In position it is extremely variable, except for the fact that it is preaxial: in *Leptodactylus* (fig. 25) and *Ceratophrys*, for example, it lies in the proximal row and articulates directly upon the radius; in the *Discoglossidæ* and *Aglossa*, on the other hand, it is invariably central, being disposed, in the former family, side by side with the postaxial centrale (figs. 4, 5, and 7), with which it seems to vie in size.

Born states (6, p. 62) that in the two "vierbeinigen Alyteslarven" previously alluded to he found "inmitten des Carpus ein freies, wohl abgegrenztes Knorpelchen von halbmondförmiger Gestalt;" he regards this as the centrale, and adds "bei zwei anderen Carpen war dasselbe mit carpale 5 verwachsen und bildete an demselben einen deutlich abgesetzten, zungenförmigen Fortsatz?" He relied, as we have before remarked, upon the section-cutter's method alone, and considering that he makes this "wichtige Fund" the basis of a revolutionary redetermination of the morphological value of certain leading constituents of the carpus (coming to regard the naviculare as a displaced radiale, and the lunatum as the intermedium), he ought, in justice to himself, to have given drawings of a complete series of sections, in place of the solitary and somewhat diagrammatic one proffered (pl. 1. fig. 5).

Born's figure shows that ossification of the metacarpals had set in, and, from the circumstances of the case, it is logical to expect that, if his observation be reliable, this supposed centrale ought to be forthcoming in younger specimens as a distinct element. We have examined a large series of specimens, many of which were much younger than any which passed through Born's hands, and they showed without exception that the position of his "centrale" was occupied by the preaxial third of that element regarded by us as the postaxial centrale (*k*, fig. 9). We can confidently assert that in no carpus under our hands does this show a trace of either segmentation into two, chondrification from two centres, or confluence of distinct elements [1].

In one specimen we have been able to detect a linear depression on the under surface of the cartilage, near the point at which Born's dismemberment appears to have occurred [2]; and we are strongly of opinion that this groove was present in his specimen, and that the section represented [3] by him passed through it. Indeed, his second assertion above cited seems, in itself, to confirm this belief.

In the adults of certain forms the naviculare may lie, as already said, more or less completely in the proximal row, preaxially to the lunatum and in more or less definite articulation with the radius (*cf.* figs. 6, 18, 30). In others it may be as fully removed from the latter (figs. 1, 5, 7). It therefore becomes a question of vital importance as to which of these two conditions is the more primitive.

In examining a large series of larvæ of the Edible Frog, measuring each about 20 mm. from snout to vent, we were not a little surprised to find that the naviculare varied greatly in the extent to which it thus embraces, as it were, the lunatum. In the adult it comes to lie in the proximal row, nearly meeting the radius (*n*, woodcut fig. B, p. 174). In a young *Bufo* of about 20 mm. it was already in direct apposition with this bone. In *Pipa* (Plate VII. fig. 1), *Xenopus* (Plate VII. fig. 4), and most *Hylidæ* (Plate VIII. fig. 20) it is strictly central; in one member of the last-named family however (*Nototrema*) it shows a tendency to become proximal in the adult.

In the adult of *Bombinator* (Plate VII. fig. 7), and still more so in that of *Discoglossus* (fig. 6), it sends up a spur which approaches but does not nearly reach the radius. Appeal to development shows (figs. 5 & 9) that this spur is a late growth.

The condition of the parts in the *Pelobatidæ* is deserving of special note. It will be seen that in those Anura in which the naviculare is most central in position the distal carpals are relatively small and reduced; in *Xenophrys* (fig. 14) and *Pelobates* (fig. 18) these are, on the contrary, larger and more nearly uniform in size with the other elements of the carpus, so much so in the latter genus that the carpus has quite a Salamandrine aspect. Here too the naviculare is proximal

[1] Ossification of this element invariably proceeds from one centre.

[2] This becomes still more marked in certain forms in which our postaxial centrale is confluent with other elements (*cf.* p. 160).

[3] There are other exceptional peculiarities about this carpus, for which we find no parallel in our own specimens.

(not strictly so in *Pelobates*), and, at the first glance, we appear to be dealing with the least modified term in the series; comparison of which with the opposite one (ex. fig. 7) would appear to show that the naviculare was primarily proximal, and that its central position has been assumed as the accompaniment of a reduction of the distal carpals.

The problem is a very perplexing one. If we admit that the Pelobatoid fore foot is the more primitive, we are forced to the conclusion that the naviculare belongs to the proximal series; if we hold the Discoglossid foot to be the more ancestral, we imply that the suppression of the carpalia is not a specialized feature [1]. In all those cases in which we have obtained sufficiently young larvæ, the naviculare is central to begin with and free of the radius, its ascending process being of secondary origin (cf. *Discoglossus*, larva and adult, figs. 5 & 6). We regard this as conclusive evidence that the naviculare does not belong morphologically to the proximal series, and hold that the condition of the Pelobatoid limb is a modified one, its naviculare having become displaced, in all likelihood at a very early stage. Nor must the possibility be overlooked that, in those forms in which the naviculare is most completely in articulation with the radius, it may have been to a large degree displaced as the direct result of enlargement of the second metacarpal (*Leptodactylus*, fig. 25), or carried up with the enlarging pollex (*Pelodytes*, fig. 11) (*cf.* p. 171). These are our reasons for regarding the naviculare as a central element, and we propose to term it, in accordance with its position, the *preaxial centrale*.

The carpus of the Anura would appear, from the foregoing, to possess two enormous centralia. Duplication or triplication of the centrale is well known in many living Urodeles. Wiedersheim [2] and Baur (1) have paid most attention to this question, and the latter has adduced weighty arguments (1, pp. 68–69) in support of the view that such duplication is purely secondary. The existence of but a solitary centrale in the lowest representatives of the Class (*Amblystoma*, Baur, p. 40), the great variation in the characters and assumed relationships of the superadded one, the occasional absence of the same (*Necturus*, *Cryptobranchus*, and others, pp. 20–29), all point to the conclusion that in this duplication we have to deal with extreme specialization. Turning now to the Anura, we make bold to assert that the hind foot of these animals is, except for its great elongation and changes incident thereon, if anything, less considerably modified than the anterior member. What, we ask, could be more extraordinary than the position in which the living *Xenopus* carries its fore foot? and may not the appearance of the second centrale have been originally associated with some such specialization? Taking all facts into consideration, we submit that, as an

[1] It is interesting to observe here that, whereas in *Alytes*, *Bombinator*, and *Discoglossus*, the ossification of the naviculare precedes that of the carpalia, in *Xenophrys* cp. 4 is the first to ossify.

[2] "Ueber die Vermehrung des Os centrale im Carpus und Tarsus des Axolotls," Morph. Jahrb. vol. vi. (1880) pp. 581–583. For other references see Baur.

Order, the Anura would appear to be unique among all living animals in that they possess, without exception, a double centrale carpi.

h. *Compound structures resulting from the fusion of two or more Carpal elements.*—Under this head we have designated certain large bones, met with only in the adults of the more specialized families and in some few isolated genera.

There can be little doubt but that the great development of our postaxial centrale (*k*) is associated with the peculiar "tread" of the fore foot of the Anura and with the remarkable distortion which the parts of this limb have undergone. In the compound structures now to be dealt with, this postaxial centrale forms as it were a central nucleus, towards which one or more adjacent elements become drawn and with which they amalgamate. The fact that the resulting compounds may occur independently in different families is sufficient to show that they are, for the most part, of nought but physiological significance.

Capitatum.—We suggest this term [1] for the simplest of the above-named structures. It occurs in *Pelodytes* (fig. 11) and *Pseudophryne* (fig. 22) (4 *k*), being formed, as shown, by the confluence of the postaxial centrale and the 4th carpal.

Capitato-hamatum.—This term was applied by Ecker (see *infrà*) to a large bone which, in the Edible Frog (3. 4. *k*, fig. B, woodcut, p. 174), carries the 3rd, 4th, and 5th digits. It is formed by the confluence of our capitatum with the third carpal.

We have observed it in the *Ranidæ, Dendrobatidæ, Engystomatidæ, Cystignathidæ, Bufonidæ, Hylidæ*, and certain others; it is not present in either the *Discoglossidæ, Pelobatidæ*, or *Aglossa*. It often sends up, especially in old individuals, a process along the outer face of the ulna (ex. *Leptodactylus*, fig. 25) for muscular attachment. This lobe is absent in the tadpole, and, from its function, it need hardly be said that it has nothing to do with articulation upon the forearm [2].

There sometimes runs along the under surface of this bone a longitudinal groove, which terminates posteriorly, in a line with the interspace between metacarpals 3 and 4. In old specimens this becomes converted into a tubular perforation, which will admit a bristle and transmits the ramus lateralis of the ulnar nerve [3].

On examination of the adult carpus, doubts might be reasonably entertained as to whether both third and fourth carpalia were incorporated in this piece. Apart, however, from the fact that in the young animal their boundary lines are definable, there is a feature of some interest in its mode of attachment. In *Hyla cærulea* (fig. 20) and *Nototrema* there still remains that ligament which, in the simpler forms, passes between the 4th carpal and the head of the 5th metacarpal; true to its relationships, it arises on a level with the head of metacarpal 4 (cf. *Xenophrys*, fig. 14), and it differs from

[1] Uniformly with Ecker's capitato-hamatum (17, p. 53).

[2] As might at first be imagined, from Wiedersheim's fig. of *Bufo* (36, pl. 211. fig. 177), in which this feature is grossly exaggerated.

[3] *Cf.* Ecker and Wiedersheim, 'Anat. d. Frosches,' part ii. p. 40 and fig. 14.

that of this genus only in that it holds the heads of metacp. 4 and 5 in apposition.

In its mode of ossification the capitato-hamatum is variable; in the Frog it ossifies in a diffuse manner, similarly to the unsegmented pollex; in some *Cystignathidæ* ossification proceeds from one definite centre.

In *Rhombophryne* (fig. 32) a still further fusion had taken place in both fore feet of the solitary specimen which we examined. This consisted, as will be seen, of a coalescence of all the central and distal elements, the two proximal ones alone remaining free. It will be shown in the sequel (p. 172) that we have observed in *Phryniscus* an unexpected range of individual variation in the fusion of adjacent elements, and we accordingly refrain from proposing a distinctive mane for this bone in *Rhombophryne*, one individual only having been at our disposal.

Postaxiale.—We propose to institute this term for an anomalous compound observed only in *Pipa* (fig. 1, *pk*). Its ascending process and all detailed relationships show that it can only be the product of a fusion between the postaxial centrale and the ulnare. With respect to this fusion *Pipa* stands alone among all known Anura whose feet we have examined[1]. The lunatum (? radiale) (*l.*) has undergone reduction consequent upon it, but we do not know sufficient of the habits of the animal to hazard a guess as to its functional significance.

III. SPECIAL PART.

A. AGLOSSA.

a. PIPIDÆ.

Examined :—

Pipa americana : large ♂ ; feet of a second adult; a young specimen 19 mm. from mouth to vent.

Fore Foot (Plate VII. figs. 1 & 2).

The radius and ulna are flat with knife-like edges, and the disposition of these bones is exceptional, in that, unlike what is seen in nearly all other Anura, the outer edge of the ulna is directed dorsally. As the result of this, the radius comes to lie in the plane of the extended hand, while the ulna lies above it.

The limb-skeleton of this genus was first described and figured by Breyer (9). Later C. Mayer, who confirmed Breyer's observations, working (28, p. 533) with wet specimens, offered certain criticisms upon the observations of Meckel (29) and showed (p. 532), with perfect accuracy, that there are six elements in the carpus. The later researches of A. J. C. Mayer and others have added but little to his description. Carpalia 3 and 4 are perfectly distinct, and it is impossible to examine these and other elements without being struck

[1] Born figures (6, pl. 1. fig. 5) a similar but incomplete fusion in the larva of *Alytes*. This we have never observed.

with the absence of that definiteness of articulation between them, met with in nearly all other Anura. *Pipa* stands alone, as before stated (p. 161), with respect to the fusion of the postaxial carpal elements; the resulting bone (*pk*) certainly includes the postaxial centrale and the ulnare, but we are unable to say whether our 5th carpale is or is not embodied. We incline to the belief that it is not. Comparison of the young and adult feet (fig. 2, *h*) shows that this compound undergoes a shortening up during development. Its postaxial lobe (* of fig. 1) is of purely physiological significance and late in origin.

Ventrally to the lunatum there is present a large lenticular bone (indicated by a dotted line in fig. 1). Baur has shown that, in the Urodele hind foot, an element of the tarsus[1] may be thus visible only on one surface, and hence we have studied with care the relationships of this element. It lies wholly out of the plane of the true carpal elements and is surrounded by tendinous tissue, while it is totally absent in the young specimen at our disposal. We regard this combination of characters as proof that it is a sesamoid.

The element marked *po.* i. is somewhat interesting. In the adult it is lenticular, and in articulation with both the naviculare (*n*) and the head of the 2nd metacarpal (2′). It might therefore appear, from its relationships, to be the carpal of the second digit. In the young specimen, however, it is exceedingly small (fig. 2) and wholly destitute of connection with the metacarpal; on comparison with *Xenopus* (fig. 4), in which the carpal of the 2nd digit is distinct, it is clear that it can only represent the carpal of the pollex[2], carpal 2 having, in all probability, become confluent with the naviculare. Examination of the young specimen (fig. 2) renders this doubtful, for the head of the 2nd metacarpal bears an enlargement, such as might conceivably have resulted from a confluence with its carpal. Upon this point we have been unable to obtain decisive evidence.

Hind Foot.

The most complete observations hitherto made upon the tarsus of this genus are those of Mayer (28). The hind foot is, like its fellow in front, very anomalous. The astragalus and calcaneus are widely separated and fused at their ends, leaving an elliptical hole in the middle; the compound thus arising is only twice as long as broad. The outer edges of the two bones—*i. e.* the preaxial border of the astragalus and the postaxial one of the calcaneus—are ridged in such a manner that each bone is T-shaped in transverse section.

The 4th and 5th metatarsals articulate directly upon the epiphysial end of the calcaneus, while the remaining three are as it were shut out from that of the astragalus by thin lamellæ of bone. These lamellæ are seen to be continuations of two out of three bones which lie on the ventral side of the tarso-metatarsal joint, and would appear

[1] Centrale 2 of *Necturus* (1, p. 20).

[2] The adult limbs at our disposal were skinned before they reached us, hence we are unable to make any definite statements concerning the pollex itself.

at first sight to be sesamoids (they were described as such by Mayer 28). The postaxial one lies altogether free of the tarsus, and it is beyond doubt, as Gegenbaur has asserted (18, p. 66), a sesamoid. The lamina of bone derivative of the middle one has all the relations of a reduced cuboideum of such an animal as the Frog; and we can only interpret the bone which gives origin to it as that structure, thrust out of position by the great development of the astralagus and calcaneus, probably as an accompaniment of the great elongation of the metatarsals.

The third or preaxial bone of the above-named series is clearly the naviculare. Firstly, it gives insertion to the tendon of the add. longus digiti I. muscle, which feature we have shown (p. 148) to be characteristic of that element; secondly, it carries a diminutive calcar of two short but ossified segments.

The young specimen examined shows no trace of distinct hallux-tarsal, nor have we been able to obtain any clue to its whereabouts.

b. Dactylethridæ.

Examined :—

Xenopus lævis: three adults; young tadpole.
Xenopus calcaratus: hind half of a late tadpole.

Fore Foot (Plate VII. fig. 4).

This carpus presents fewer anomalies than that of *Pipa*. The ulnare (*p*) is quite distinct and in no sort of fusion with the postaxial centrale (*k*). Our fifth carpal is wanting, but those of the four remaining digits are large and distinct. The naviculare (*n*), is in its large size and in the possession of a preaxial spur, quite unlike that of *Pipa*.

As in *Pipa*, the metacarpals are greatly elongated; this genus is exceptional, however, in the great expansion of the head of the 4th one (4′) and the excavation of that of the 5th for the reception of a special peg of the postaxial centrale (*k*).

The lenticular sesamoid (indicated in a dotted line) lies, in this genus, in the line of junction between the radius and ulna, instead of being preaxial as in *Pipa*.

Hind Foot (Plate VII. fig. 3).

The astragalus and calcaneus are much more normal than in *Pipa,* their extremities are very broad (fig. 3), and the distal epiphysial cartilage ossifies from three independent centres (see fig. 3).

There overlies the head of the second metatarsal a small bone (1) which is wedged in between it and the centrale (naviculare *n*′); we regard this as the tarsal of the *hallux*, for reasons already given (p. 146) in dealing with the same condition in *Bufo* and the Tree-Frog. The bone marked $^{2\ 3}$ we accordingly hold to represent the fused tarsalia of the 2nd and 3rd digits.

The metatarsals are much elongated and the head of the third one (3′) is exceptional for its great breadth; seeing that the tarsals are complanate with these and not displaced ventrally, it follows that the hind foot is here, like its fellow in front, much more normal than that of *Pipa*.

The calcar consists of three slender elements, the proximal one of which can only represent a tarsal.

B. PHANEROGLOSSA.

a. Discoglossidæ.

Examined :—

Discoglossus pictus : adult ♂, a young specimen, and a tadpole.
Alytes obstetricans : } large series of adults and tadpoles.
Bombinator igneus : }

Fore Foot (figs. 5, 6, 7, 9).

Born's latest communication upon the fore foot in *Alytes* (6) would be little short of revolutionary could his deductions be substantiated. We have already fully discussed these (p. 157), giving our reasons for rejecting them *in toto*.

The general plan of the carpus in these three genera is very similar; in all, the largest element of the series is our postaxial centrale (*k*), and it is in this that ossification first commences. Gegenbaur has already called attention to the fact that in *Bombinator* it is "nicht gar schwer" to see in the naviculare (*n*) the centrale of the Urodela; we have already given our reasons for regarding this element as a preaxial centrale (p. 159).

Gegenbaur says that in *Bombinator* (18, p. 17) all the carpal elements are distinct; we, however, interpret the 5th carpale of all our predecessors as a postaxial centrale (p. 157). Concerning the remaining carpalia we are at variance with Born; he figures an individual *Alytes* larva in which carpale 4 appears to have fused, while still cartilaginous, with cp. 5 (our postaxial centrale)—this we have never observed. He also states that in *Bombinator* a similar confluence may occur between carpalia 2 and 3 while still cartilaginous; and he remarks that these variations "auf eine Neigung zum Uebergang in die für *Rana, Bufo* u. s. f. characteristische Carpüsform schliessen lassen." We have searched most carefully for traces of any such fusion, with negative results; carpalia 1, 2, 3, and 4 being throughout distinct in all our specimens. These elements remain for a long time unossified in *Alytes* (fig. 9), they ossify in order 1, 4, 3, 2; in the interval, however, between the ossification of our postaxial centrale and these carpalia, the naviculare, ulnare, and lunatum ossify in the order named. The following is the formula for the whole series:—

k. *n*. *p*. *l*. 1, 4, 3, 2.

The carpal of the 5th digit is represented in all three genera by the ligamentous band previously described (p. 154); in *Alytes* this carries a tolerably large cartilaginous nodule, which we regard as the vestige of the 5th carpale of the Urodela.

According to Born (6, p. 62) the rudimentary pollex may, in *Bombinator*, either bear two phalanges or be wholly absent. In all our specimens we find that it bears two segments (*po.* ii. & iii.), irrespective of its carpal (*po.* i.). In *Discoglossus* and *Alytes* there is but one segment other than the carpal present; in the male *Discoglossus* this becomes fully ossified and expanded.

During ossification of the leading elements in *Discoglossus*, a central deposit takes place in each (*l. n.* fig. 5); soon, however, a differentiation of the ossific centre into a superficial spongy annulus and a central denser core takes place (*pk*, fig. 5), leading up to the curious condition of the adult bones (fig. 6) already noted (p. 143).

Hind Foot (figs. 8 & 10).

Gegenbaur was in error in asserting (18, p. 60) that in *Bombinator* the separation between the astragalus and calcaneus is complete. In even the youngest larva examined by us these two elements had already become confluent, bearing a common expanded epiphysial cartilage.

Born claims for the same genus (6) a range of individual variations in the tarsalia far exceeding anything which we have observed. In all our specimens the tarsalia of digits 1, 2, & 3 are distinct, that of the third being invariably the largest. Tarsalia 4 & 5 are represented by a ligament, which in *Alytes* alone carries a nodule of hyaline cartilage (p. 145).

The naviculare (centrale, *n'*) is, in all, large, and so placed as to separate the hallux-tarsal (1) from the astragalus, the epiphysial end of which is excavated so receive it. This element is always the first to ossify, the calcar follows, tarsalia 1, 2, 3 remaining for a considerable time unossified.

The calcar never consists of more than two segments, and is in all small. Born, in opposition to Leydig, regards the solitary piece present in *Alytes* (fig. 10, *ph.* i.) as the metatarsal (our tarsal) + the phalanx of the sixth toe. We have been unable to detect the presence, at any stage, of a second segment; we hold, therefore, that the element in question is really the hallux-tarsal.

b. PELOBATIDÆ.

Examined:—

Xenophrys monticola: 3 specimens measuring respectively 70, 40, and 26 mm.
Pelodytes punctatus: 3 adults and a tadpole.
Pelobates fuscus: an adult ♂ and one very young specimen.

Fore Foot (figs. 11, 14, 15, 16, 18).

That which most characterizes the carpus in this family is the relatively large size of the four carpalia (*cf.* p. 158). The 5th carpal is represented in a ligament, the detailed relationships of which have been already described (p. 154). This, as will be seen in fig. 15, becomes suddenly constricted at its point of insertion into the head of the outermost metacarpal, especially in *Xenophrys*, in the adult of which it carries a distinct bony element (5, fig. 16), regarded by us as a 5th carpal (p. 154). It is worthy of remark that in its mode of ossification this element conforms in every detail to that observed for the other capalia.

Born asserts that he found (6, p. 63) in a *Pelobates* larva a centrale carpi, identical with that figured by him in the young of *Alytes*; and he expresses his doubts as to whether the same does or does not regularly fuse with the 5th carpal (our postaxial centrale, *k*) in the adults of both genera. It must suffice to point out that we have not here observed the presence of that cartilage which he calls the centrale, and the statements already made by us for *Alytes* (p. 158) apply equally to this genus.

This preaxial centrale (naviculare, *n*) may or may not reach the radius in individuals of a species. In the *Pelobates* figured (fig. 18) it is represented as nearly touching that bone, but in the other carpus it did not extend more than halfway towards it. We have already stated (p. 159) our reasons for regarding this ascending lobe of the naviculare as purely secondary.

Extremes of modification of the pollex are met with within the limits of this small family. In *Pelobates* and *Xenophrys* it consists, excluding its carpal (*po.* i.), of a small styliform structure which is quite unsegmented; in *Pelodytes*, on the other hand, it is very large and swollen (fig. 11, *po.* i.–iii.) and definitely segmented. In all three genera the rotation of the hand upon the fused radius and ulna is very marked; and in *Pelodytes* this reaches its maximum, having gone on through more than a right angle (fig. 11). Comparison with the other two genera suggests that the great development of the pollex may be in some way associated with this distortion; and we are inclined to ascribe to the same cause a distinct ossification of the distal extremity of the ulna here met with (* of fig. 11)[1].

In *Pelodytes* the carpus is exceptional among those of this family, owing to the fusion of the postaxial centrale and fourth carpal to form one bone, the capitatum (4. *k*, fig. 11).

Hind Foot (figs. 12, 13, 17).

It is interesting, in the light of the facts concerning the fore foot, to note that the extremes of modification undergone by the astragalus and calcaneus in the Anura are exemplified in this family. In *Pelodytes* (fig. 12) they are confluent for their whole lengths, much elongated and slender in the middle; in *Pelobates* they are relatively shorter than in any Frog which has come under our notice. *Xenophrys* is, in respect to relative length, intermediate between the two.

The calcar (pre-hallux) attains, as is well known, its maximum development in this family. Rosenhof first described and figured

[1] This is not received by the ulnare, as might appear on examination of the figure; it lies, in life, ventrally to the line of junction between that bone and the lunatum. It breaks away with great readiness, so much so that we originally imagined it to be a distinct element.

its skeleton (32), and Gegenbaur, Born, and Bayer (2) have more recently redescribed it. Born states that in the larva of *Pelobates* it possesses two phalanges (6, p. 59)—that is to say, there was originally a second segment added to that which we regard as its metatarsal. While we have not seen this ourselves we are able to record the presence of such a phalanx in *Pelodytes* (*ph.* iii. fig. 13), attached at right angles to the metatarsal (*p.h.* ii.). In *Xenophrys* the pre-hallux is relatively small, consisting of a single piece (fig. 17, *p.h*) which ossifies late.

The calcar of *Pelobates* is set on at right angles to the plane of the foot, and, in displacing it for examination side by side with adjacent parts, most observers have hitherto dislodged tarsalia 1 and 2 from their natural connexions. Born first described the hallux-tarsal in this animal (3, p. 446); and we have already shown (p. 148) that its relationships to the basal segments of the pre-hallux in *Pelodytes* necessitate a revival of the older view concerning the morphology of the naviculare. In *Xenophrys* the hallux-tarsal is very large and lozenge-shaped, being wedged in (fig. 17, I) between the heads of the 1st and 2nd metatarsals.

With respect to the remaining tarsalia we find, in this family, as with the carpalia, an inconstancy. While in *Pelodytes* and *Pelobates* tarsalia 2 and 3 are quite distinct, in *Xenophrys* (fig. 17, ^{2} ^{3}) they unite to form the "cuboideum" so well known in the Common Frog. In young specimens this bone is in articulation with the outer half of the head of metatarsal 2, but in the adult it becomes shortened up in a manmer suggestive of *Hyla* (p. 146 & fig. 19).

The ligamentous representative of the 4th and 5th tarsals is well marked in all three genera. We are unable to reconcile the description and figures of this and the third tarsal given by Bayer (2), either with each other or with the feet at our disposal.

c. Hylidæ.

Examined:—

Hyla peronii; *H. freycineti*; *H. lichenata*; 2 *H. ewingii*; 5 *H. cærulea*; *H. albopunctata*; 5 *H. arborea*, tadpoles.
Nototrema marsupiatum.
Phyllomedusa hypochondrialis: small specimen.
Phyllomedusa dacnicolor: large specimen.

Fore Foot (fig. 20).

The characters of both fore and hind feet are very constant throughout this family. The rotation of the fore foot upon the fused radius and ulna is, in all, very marked. The naviculare is central in position in all but *Phyllomedusa* and *Nototrema*, in which two genera it sends up a radial spur which we have shown to be secondary (p. 159).

The carpalia 3 and 4 have coalesced with the postaxial centrale to form a capitato-hamatum as in the common Frog (3, 4, *k*, fig. 20), upon which digits 3, 4, and 5 articulate. This family is unique in respect to the retention, subsequent to the incorporation of the 4th carpal in this bone, of that ligament (* fig. 20) which, in the simple forms, represents the 5th carpal (*cf.* p. 160). In *Xenophrys* (fig. 15) it will be seen that the fourth carpal is wedge-shaped postero-externally, extending over the inner half of the head of the fourth metacarpal; it is from this point that the ligament in question arises in both *Xenophrys* and *Hyla*, and we hold this as proof conclusive that the 4th carpal is, in the latter, represented in the manner described.

Carpalia 1 and 2 are both distinct, the carpal of the pollex being elongated and slightly constricted in the middle (*po.* i. fig. 20).

The pollex itself varies in degree of development; its topographical value has been discussed by Cope and others (14, p. 200). Structurally it consists essentially of one piece (excluding its carpal) which may show traces of differentiation or constriction into two segments (*po.* ii., fig. 20). In the American Tree-Frogs with "external pollex" (*Hyla albopunctata*) the parts differ only in being very broad.

Hind Foot (figs. 19, 21).

As previously pointed out (p. 146), examination of the adult tarsus (fig. 19) would lead to the supposition that the tarsal of the hallux is absent, and that the two bones which are nearest related to the heads of the metatarsalia 2 and 3 represent their tarsals alone. In fact Gegenbaur (18, pl. 6. fig. 9) was led into this belief. Comparison of the larva shows that this is not the case, but that the outer of the two elements, when it first appears, has all the characters and relationships of the "cuboideum" [1] previously described in the *Pelobatidæ*. This bone is present in all the *Hylidæ* which we have examined, and it is characteristic of this and all the succeeding families.

The astragalus and calcaneus are greatly elongated (*cf.* Hofmann, 21, pl. 14. fig. 10) in all, and their epiphysial cartilage is generally enlarged for special articulation of the 4th metatarsal (*cf.* fig. 19); as the result of this, these bones come to be inclined at a considerable angle to the metatarsals.

The central portion of the epiphysis is ossified near the astragalar border (fig. 19) at the point of attachment of a powerful ligament, which is inserted at its outer end into the wall of the articular capsule and carries at its point of insertion a cartilaginous nodule. In old specimens this may become ossified, and we believe, for reasons previously given (p. 146), that it is an adaptive structure of no morphological importance, having nothing whatever to do with the missing 5th tarsal. There is no trace of it in the tadpole.

The naviculare is present as a distinct element in all (*n'*, figs. 19, 19 *a*), lying in a line with the pre-hallux tarsal (*ph.* i.). In *Phyllomedusa* it is unusually small, being barely larger than the tarsal of the hallux.

[1] *Cf.* p. 146.

The pre-hallux is present in all specimens examined by us [1], and it consists in them of four segments—a proximal larger one or tarsal (*ph.* i.), a smaller metatarsal, and two diminutive phalanges [2]. The retral process of the second or metatarsal segment (* of fig. 19) is absent in *Phyllomedusa* (fig. 19 *a*). In an old specimen of *Hyla lichenata*, on the other hand, it was completely segmented off on either side, forming (woodcut, fig. A, p. 151) the largest of a series of nodules which fringed the free border of the pre-hallux fold. We have already discussed the probable significance of these.

d. Bufonidæ.

Examined :—

Bufo vulgaris.
Bufo viridis : large specimen.
Bufo calamita: 8 young.
Bufo variegatus : young.
8 *Pseudophryne bibronii.*

Fore Foot (fig. 22).

The limb-skeleton of *Bufo* has been described by various authors; it was first figured by Brandt and Ratzeburg (8), and subsequently by Mayer (27). Gegenbaur, Owen, Born, and Wiedersheim have in turn dealt with this skeleton, and upon some of their observations we have already commented.

Pseudophryne (fig. 22) is exceptional among the members of this family in the characters of its carpus : in *Bufo* the naviculare (*n*) articulates directly with the radius, and lies in the proximal row, here it is comparatively small and central : in *Bufo* the 3rd and 4th carpalia and our postaxial centrale coalesce to form a capitato-hamatum, as in the Common Frog. In *Pseudophryne* there are three carpals lying to the inner side of the large capitatum (4 *k*), whence it follows that cp. 3 is distinct as in *Pelodytes*. The carpus of *Pseudophryne* approximates more nearly towards that of *Pelodytes* than any other genus yet examined; and considering that the *Bufonidæ* are, with respect to the confluence of their distal and postaxial central elements, a stage in advance of the *Pelobatidæ*, *Pseudophryne* is to them what *Pelobates* is to the latter.

Hind Foot (fig. 23).

We can confirm Born's statements concerning the tarsalia in this family (3, p. 443) regarding the homology of the element marked (2, 3) with the tarsalia of the second and third digits, and we find that in old specimens this may become shortened-up in a manner suggestive of the Tree-Frogs. We have nothing to add to what we have already stated in confirmation of Gegenbaur's observations concerning the ligamentous 4th tarsal (*cf.* p. 145).

[1] Leydig states that he was unable to find its cartilages in *H. arborea* (25, p. 181).

[2] Born has described and figured the details of ossification of these, subsequent to fusion, in a very old specimen of *H. arborea* (6, pl. 1. figs. 1 and 2).

Born records (6, p. 55) individual variations in the constitution of the pre-hallux; we agree with him only so far as concerns the presence of three segments irrespective of our tarsal one (*cf.* p. 149). The terminal one of these is never recognizable in the adult (fig. 23), and we have failed to find it in *Pseudophryne*.

e. CYSTIGNATHIDÆ.

Examined:—

5 *Limnodynastes tasmaniensis*; *L. dorsalis.*
Leptodactylus pentadactylus: 140 mm.
Leptodactylus albilabris: 23 mm.
Ceratophrys ornata: 140 mm.
Ceratophrys americana.
Chiroleptes australis.
Crinia varia.
3 *Pseudis paradoxa*, tadpoles.
2 *Hylodes martinicensis.*
Telmatobius jelskii, tadpole.
Paludicola bibronii.
4 *Heleioporus albopunctatus.*

Fore Foot (figs. 25, 26, and 28).

Gegenbaur (18) and Hofmann (21) have alluded casually to the limb-skeleton of one or two genera of this family; but the most complete account yet published is that of Mayer (27).

The skeleton of the fore foot resembles, in its general aspect, that of the Frog; and in a family where three of the eight carpal elements are invariably fused together (capitato-hamatum, 3, 4 *k*) there is little room for modification of any morphological importance. The carpus of *Limnodynastes* (fig. 28) may be conveniently taken as a type of the whole family. The naviculare (*n*) lies well towards the radius, being prolonged forwards into a thin edge. The pollex carpal is free and little modified, carrying the pollex (*po.* ii.). This consists of a single element which is, in the male, shovel-shaped and beset by a horny investment, much in the manner of the calcar in *Pelobates* or *Heleioporus*.

The following are the more important departures from the above that we have observed in the genera recorded:—

Pseudis (fig. 26).—The second digit is remarkable for its slenderness, while it is closely related to the pollex, and, with it, opposable. This change is accompanied by a corresponding increase in calibre of the head of the 3rd metacarpal (3′). The carpal of the pollex is greatly elongated, in excess even of that which is seen in the *Hylidæ*.

Ceratophrys.—The naviculare here lies in the proximal row, and offers a broad surface for articulation with the radius. The carpal of the pollex is stouter than that of the second digit, and it bears two short, but well-defined and fully ossified, segments[1].

Leptodactylus.—The naviculare is here in full articulation with

[1] This is also the case in *Paludicola.*

the radius (fig. 25). The pollex consists of two short segments, borne upon an equally insignificant carpal (*po.* i.–iii.), the whole standing out at a right angle to the long axis of the fore foot. In the male the head of the second metacarpal is, as Mayer has shown (27), immensely enlarged for support of the horny clasper (** fig. 25).

It would appear, at first sight, that the displacement of the naviculare might have been the direct outcome of this enlargement; but if so, the reduction of the 2nd carpal to the condition of an absolutely insignificant nodule (2) becomes unintelligible, for it certainly would appear that that must have resulted from the same cause. We find, in the young specimen at our disposal, that this is really the case, for in the absence of the clasper the 2nd metacarpal is relatively larger. It is interesting to note further, that while, in this specimen, the naviculare does not quite reach the radius, the pollex is proportionately much stouter than in the adult. On consideration of these facts we incline to the belief that the displacement of the naviculare was originally associated with the enlargement of the pollex, in a manner similar to what is seen in *Pelodytes* (fig. 11), and that with the reduction of the pollex its connection with the radius became lost, only to be resumed again on the great enlargement of the 2nd metacarpal.

In the male of *Limnodynastes* the preaxial border of the second metacarpal bears an irregular bony crest, like that of the Common Frog. We find, however, that the pollex never here fuses with this, as it may do in the last-named genus.

Hind Foot (figs. 24, 27, and 29).

The typical condition of the Cystignathid hind foot is exemplified in *Cystignathus* and *Limnodynastes* (fig. 29), and, as the figure shows, it is, in general, Frog-like—*i. e.* tarsalia 2 and 3 are fused to form a single cuboideum ($^{2\ 3}$). In *Leptodactylus* this splint is shortened up, so that the hallux-tarsal nearly equals it in size.

In *Ceratophrys* the hallux-tarsal is absent, having either fused with the naviculare or disappeared, as believed by Born (3, p. 441) for *Rana*.

The calcar is, like the pollex, subject to no inconsiderable variation, as might indeed be expected of a family whose members lead such diverse modes of life. In *Ceratophrys* (fig. 24), *Cystignathus*, and *Limnodynastes* (fig. 29), we have only been able to recognize two segments, the basal one of which represents the tarsal (*ph.* i.), while in *Leptodactylus* the full complement of four pieces is reached.

Pseudis (fig. 27) bridges over the interval between these two conditions, in that a small first phalanx is present (*p.h.* iii.). In this animal the middle or metatarsal segment greatly exceeds the basal one in length, and its proximal outer border is enlarged; in *Limnodynastes* this enlargement becomes more obvious, leading up to the condition seen in *Ceratophrys ornata* (fig. 24), where it assumes the form of a retral spur[1].

[1] This is very feeble in a smaller specimen of *C. americana* examined.

In *Cheiroleptes* the proximal segment is by far the stronger; while in *Heleioporus* the second one is robust and forcibly reminds one of the calcar in *Pelobates*.

f. Engystomatidæ.

Examined:—

Rhinoderma darwini.
Phryniscus lævis, *varians*, and *cruciger*, several.
Brachycephalus ephippium.
Callula picta; *C. baleata*.
Microhyla, ? sp., 2.
Rhombophryne testudo.

Fore Foot (figs. 30, 32).

The carpus in this family stands boldly out from that of all other Anura, with respect to the extraordinary tendency towards fusion of more or fewer of its elements with each other or the adjacent metacarpals.

The naviculare shows a tendency to become proximal in all; in *Phryniscus* (fig. 30) its ascending spur is strongly marked, nearly meeting the radius[1]. This bone is implicated in the simplest fusion observed (*Microhyla*), becoming confluent with the lunatum. If our determinations of the morphological value of the carpal elements are sound, it follows that in this almost unparalleled feature we have the precise converse of the unique phenomenon encountered in *Pipa* (p. 162)—there, our postaxial centrale is in confluence with the proximal postaxial element; here, the preaxial one enters into similar relationship with the proximal preaxial bone.

Brachycephalus[2] stands alone, among all forms examined by us, in that carpale 2 early unites with its corresponding metacarpal.

The above simple cases fade into insignificance beside that of *Rhombophryne*[2] (fig. 32). Here, all four carpalia and our two centralia have become welded into one great mass, interposed, as it were, between the lunatum and ulnare and the heads of the metacarpals. The boundary lines of its originally distinct constituents may be, for the most part, followed.

Remarkable indeed is the condition met with in *Phryniscus*, for here the variations are not even generically constant. In the two specimens of *P. lævis* examined, all the parts were free (fig. 30), while in *P. varians* carpale 2 had fused with the naviculare. In *P. cruciger* we found a unique state of affairs, carpals 1 & 2, metacarpals 1 & 2, and the naviculare all being firmly anchylosed together. It will be observed that here, as in *Microhyla* and less conspicuously in *Brachycephalus*, the whole tendency is towards imparting rigidity to the preaxial limb-border; it is not surprising, therefore, to find the naviculare sending up a radial spur, and, in doing this, appearing to become proximal.

[1] As already pointed out by Gegenbaur (18, p. 17).
[2] One specimen only examined.

Attention has already been called by one of us [2] to the existence of unexpected specific and even individual variations in the larynx of certain Anura; and we anticipate that a similar range will sooner or later be demonstrated for those in the carpus of this family, if of none other.

The pollex consists, in all specimens with which we have dealt, of one piece, irrespective of its carpal. In *Phryniscus lævis* this structure recalls (*po.* ii. fig. 30), as does the 'hand' generally, the condition of the Common Frog. In *Rhombophryne* (fig. 32) it is broad and calcariform.

Hind Foot (figs. 31 & 33).

In this we meet with variations little less surprising than those of the fore foot. The astragalus and calcaneus are in *Phryniscus lævis* widely separated (*a.*, *c.*, fig. 31); in *P. cruciger* and *P. varians* they lie close together as in the Tree-Frogs.

The hallux-tarsal is variable in the extreme in its relationships. In *Brachycephalus*, *Microhyla*, and *Rhombophryne* (fig. 33 [1]) it is distinct and of fair size; in *Phryniscus cruciger* it had fused with the naviculare; while in the solitary specimen of *P. varians* examined it was confluent with the os cuboideum (tarsalia 2 and 3).

The calcar consists, in its simplest condition (*Brachycephalus*, *Microhyla*, *Phryniscus varians*, *Rhinoderma*, *Rhombophryne*, fig. 33) of two elements. In *Phryniscus cruciger* these had anchylosed, but in the young of *P. lævis* figured (fig. 31) four distinct elements were discernible.

It is worthy of remark that the anterior of the two ligaments which we record for the *Hylidæ* (p. 168, Plate VIII. fig. 19) reappears here with its contained sesamoid cartilage.

g. Dendrobatidæ.

One specimen of *Dendrobates tinctorius* was examined, but its carpus and tarsus correspond so closely with those of the Frog that it is needless to describe them separately.

h. Ranidæ.

Examined:—

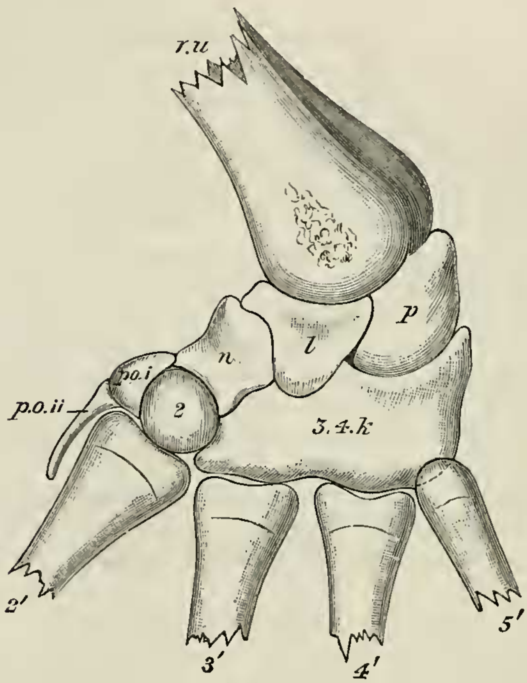
Rappia marmorata.
Nannophrys ceylonica.
Rhacophorus maculatus; *R. eques.*
Ixalus leucorhinus.
Cornufer vitianus.
Megalixalus madagascariensis.
Rana alticola; *R. cyanophlyctis*; *R. arvalis.*
Rana esculenta; *R. temporaria*: a large series of specimens at all stages.

There is a marked constancy in the carpus and tarsus of this

[2] P. Z. S. 1887, pp. 491–501.

family, and with the exception of a broadening of the pollex in *Cornufer* and *Rhacophorus*, and an increase in size of the proximal end of the pre-hallux metatarsal segment in the first-named genus, we have met with no important departure from what is seen in the Common Frog. As this animal is so largely in demand for ordinary class use[1], we append a somewhat detailed description of its limb-skeleton, in the light of our preceding observations.

Fig. B.



Rana temporaria, ♀, 54 mm. in length.
Left fore foot, dorsal view, × 12. The coalesced radius and ulna (*r. u*) are represented in the natural position. For references see p. 182.

Fore Foot (*Rana temporaria*).

In the adult carpus of this animal, six bones may be recognized, all of which are in their original positions with the exception of the naviculare (*n*). This has, as already remarked (p. 158), undergone elongation and displacement radially. We were not a little surprised to find that there is considerable variation in the position of this element in young Frogs, whose carpus and tarsus were still unossified. In a large series of specimens examined, measuring at

[1] The descriptions given in the students' manuals (Huxley & Martin's 'Elem. Biology,' Marshall's 'Frog,' and Mivart's 'Common Frog') are for the most part compilations, and we deem it unnecessary to criticise them in detail.

most 18 to 20 mm. in length, it flanked from one-third to three-fourths of the preaxial border of the lunatum. In these, as in the adult (fig. 2), it is four-cornered as seen from the dorsal aspect; in old Frogs it becomes triangular and it may fuse with the lunatum, in the manner already described (p. 172) for *Microhyla*.

The *lunatum* (*l.*) articulates proximally with the epiphysial border of the radius, preaxially with the naviculare by a concave or flattened surface, and postaxially with the proximal half of the inner border of the ulnare (pyramidale)—between it and the distal half of this bone the foramen intercarpi is enclosed (*cf.* p. 156).

The *ulnare* (*pyramidale*) (*p.*) is in articulation proximally with the ulna and distally with the large capitato-hamatum (3, 4 *k*) of the distal row; the hinder half of its preaxial border is free, as above stated. The articulations of this element are of a loose order with the exception of that associated with the capitato-hamatum; this bears antero-ventrally a projecting socket, which is excavated to receive a corresponding and prominent downgrowth of the ulnare.

Looked at *in situ*, with the fore foot in the extended position, the lunatum is most dorsally extended, and the ulnare most ventrally so. Examination of the parts thus shows that, while the rotation of the fore foot upon the radius and ulna has affected the articulation between these bones and the proximal carpals as a series, it has also brought about a less conspicuous rotation of the proximal upon the distal carpal elements.

Capitato-hamatum (3 4 *k*).—It is needless to recapitulate the grounds upon which we have come to regard this as a compound of the 3rd and 4th carpalia of previous workers with our postaxial centrale. Postaxially it sends up a lobe which embraces the free border of the ulnare, much in the manner of the secondary relationship assumed between the naviculare and lunatum. Proximo-internally it articulates with the naviculare, lunatum, and ulnare, distally so with the metacarpals 3, 4, and 5, by special condyles. This compound transmits ventrally, in the adult, the lateral ramus of the ulnar nerve; the foramen through which that passes is, in young animals, represented by an open groove (*cf.* p. 160).

Carpal of 2nd digit.—This element (^{2}) varies considerably in shape, being sometimes rectangular, at others convex on all sides and approximately spherical.

Carpal of the pollex (^{1}).—This is more fully represented than might be imagined, on a knowledge of the great reduction of the pollex itself. It is strongly convex externally, and concave internally, for articulation upon the carpal of the second digit and the naviculare respectively.

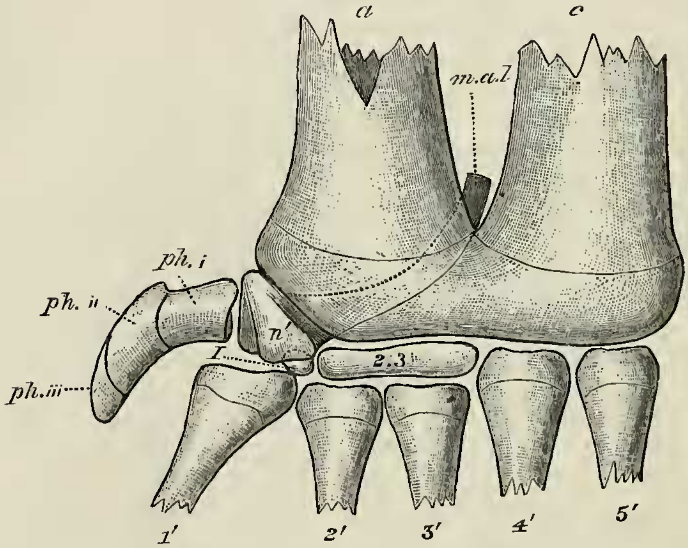
Pollex.—This is invariably in a vestigial condition, consisting in the adult (see woodcut, fig. B) of a single piece, excluding its carpal, with which it is in definite articulation by a facet. Applying arguments previously adduced (p. 149), we regard this structure as representative of the entire first digit, rather than of its metacarpal alone as is more generally and empirically asserted.

Metacarpals.—In the male the metacarpal of the second digit becomes modified preaxially in connection with the thumb-pad. We have nothing to add to Leydig's account of this feature (26). The heads of the 2nd, 3rd, and 4th metacarpals are expanded and more or less considerably excavated, for articulation upon the carpalia and the capitato-hamatum. The head of the 5th metacarpal is, like its shaft, comparatively very slender, while it is so modified as to embrace the postero-external angle of the capitato-hamatum in the manner of a pincers apparatus.

Hind Foot (Rana temporaria).

The astragalus and calcaneus (*a.*, *c.*) are much elongated, confluent at their extremities, concave internally, and either circular or elliptical in section. Their internal borders bound the limits of origin of the adductor longus digiti primi muscle, the tendon of which (*m.a.l.*)

Fig. C.



Rana temporaria, ♀, 54 mm. in length.
Left hind foot, dorsal view, × 12. *m.a.l.* tendon of the adductor longus digiti primi muscle. Other references as at p. 182.

is inserted into the naviculare (*n'*). With the full development of this there arises from the epiphysial cartilage of the astragalus a prominence which overlies the tendon[1], and which ossifies with age; in old individuals there passes between it and the calcaneus an annular ligament.

Tarsalia 4 *and* 5.—Represented in ligament, which is not recognizable in adult specimens.

Tarsalia 2 *and* 3.—Invariably united to form the splint-like

[1] *Cf.* Ecker (17, p. 128, and fig. 91).

"cuboideum" (2, 3). This compound is interposed between the astragalus and the heads of metatarsals 2 and 3.

Naviculare (*centrale*), *n'*, and *hallux-tarsal.*—The former articulates obliquely upon the epiphysial cartilage of the astragalus; its outer face bears two convexities of nearly equal size, which are separated by a shallow groove. The ventral convexity furnishes the main articulation for the pre-hallux (see woodcut, fig. C).

The hallux-tarsal (*I*) is generally, though not invariably, present; when recognizable as a distinct element it assumes the form of a small nodule of cartilage, lying buried up in a confused mass of ligamentous tissue, in the interspace between the postaxial hinder border of the naviculare, the head of the hallux-metatarsal, and the os cuboideum (*cf.* p. 147). In the Bull Frog (*R. pipiens*) this cartilage ossifies, but we have never observed that to be the case in *R. temporaria.*

Pre-hallux (*calcar*).—Born admits the existence of from 2 to 4 pieces in this structure (*cf.* p. 149), while he records (5, p. 233) the presence of three[1] such in *R. arvalis*, in contradistinction to Leydig.

In young Frogs of 20 millim. in length we find four distinct segments of hyaline cartilage. The first or tarsal segment (*ph.* i.) articulates with the naviculare; the second or metatarsal one is the largest, and bears a small retral process; of the third and fourth or phalangeal segments, the latter undergoes degradation and is represented only in ligament in the adult. The three persistent segments ultimately undergo ossification and usually remain distinct.

IV. Conclusions.

Fore Foot.

1. That the pyramidale represents the ulnare, and that there is insufficient evidence upon which to base a final determination of the morphological value of the lunatum.

2. That the naviculare is a preaxial centrale, and that its connection with the radius is always secondary.

3. That a vestigial 5th carpal is present in the adults of the *Discoglossidæ* and *Pelobatidæ.*

4. That that element hitherto regarded as the 5th carpal is a postaxial centrale, and that the living Anura are unique, as an Order, in the invariable possession of two large centralia carpi.

Hind Foot.

5. That no traces of a third proximal tarsal element are forthcoming at any stage in development; and that the morphological value of the astragalus and calcaneus has yet to be settled.

6. That while the tarsalia of the 4th and 5th digits are often represented in ligament, skeletal vestiges of the fourth one are forthcoming in the *Discoglossidæ.*

[1] Four actually; but it will be remembered that he regards our centrale (naviculare) as the pre-hallux tarsal.

7. That the naviculare is a centrale and not the basal segment of the pre-hallux.

8. That the pre-hallux never consists of more than four pieces, and that it conforms to the structural requirements of a sixth digit.

9. That the outer free border of the pre-hallux may undergo a process of fragmentation, giving rise to insignificant nodules of cartilage indistinguishable from those for which, in certain other Vertebrata, the value of lost rays has been claimed; and that the grounds upon which this claim is based are unsatisfactory.

10. That there is a tendency towards loss of independence of the hallux-tarsal in the *Discoglossidæ*, *Pelobatidæ*, and some *Ranidæ*, that element in them remaining cartilaginous and small, or fusing with one of the adjacent elements.

11. That *Pipa* is alone exceptional among living forms, in that the third digit exceeds the fourth one in length.

Perusal of the body of this paper will show that in all the higher families of Anura there is a general tendency towards confluence of three or more of the carpal elements, but consideration of the fact that such modifications by fusion may not be even generically constant, shakes our faith in them as guides to affinity. The fact which stands out most conspicuously is that the least modified conditions of both fore and hind feet are most nearly combined in the *Discoglossidæ*. Hochstetter has recently shown (20) that in *Bombinator* the posterior cardinal veins are retained for life, in a slightly modified form, and his observation has been supplemented by one of us and extended (22) to *Alytes* and *Discoglossus*. Adding these facts to those so well known concerning the vertebral and other characters of this family, there can no longer be any doubt that its members are, by far, the least modified of all living Anura.

The digital formula of the Anura is [1]:—

Fore.	Hind.
Ph. 2, 2, 3, 3.	Ph. 2, 2, 3, 4, 3.

The only other Amphibia of which we have any knowledge whose phalanges approach this in order of arrangement are the Stegocephalia of the Permian. We unfortunately know nothing of their carpus and tarsus. Baur has lately tabulated (1, p. 64) the digital formulæ of all known Urodela, and perusal of his tables will show how completely all the members of that order are, in this respect, modified as compared with the Anura. Thus it is seen that while the limb-skeleton of the Frogs and Toads is specialized in the extreme for physiological purposes, there is retained in it a leading morphological feature which carries us back to some of the oldest known representatives of the class Amphibia; and we must look to the Stegocephalia themselves or to some closely allied forms for the ancestors of these familiar creatures.

[1] During the passage of these pages through the press, Mr. Boulenger has called attention (see below pp. 204–206) to the fact that in certain *Ranidæ* a supernumerary phalanx is intercalated between the penultimate and terminal ones of each digit in both fore and hind feet. The formula of these animals is thus: 3, 3, 4, 4. 3, 3, 4, 5, 4.

Walterstorff has recently published (37, 38) an exhaustive account of certain fossil frogs, and of the Palæobatrachidæ in particular. He claims to have discovered a series of connecting-links between the Arcifera (*Pelobatidæ*) and the Aglossa. He has pointed to the equality in length of the 3rd and 4th digits of the hind limb in certain of his specimens, and his deductions receive additional support from the fact that in some of those the third digit appears to have even exceeded the fourth in length, as we have shown to be the case in the living *Pipa*.

V. List of Authorities referred to.

1. Baur, G.—Beiträge zur Morphogenie des Carpus und Tarsus der Vertebraten. 1 Theil. Batrachia. Jena (1888).
2. Bayer, F.—Ueber das Skelett der Pelobatiden. Abhandl. d. köngl. böhmischen Gesellschaft, vol. xii. (1883–84), pp. 1–24, German abstract.
3. Born, G.—Die sechste Zehe der Anuren. Morph. Jahrb. vol. i. (1875) pp. 435–452.
4. Born, G.—Zum Carpus und Tarsus der Saurier. Ibid. vol. ii. (1876) pp. 1–26.
5. Born, G.—Ueber des Skelett des Tarsenhöckers v. *Rana fusca* und *R. arvalis*. Stzb. der naturwiss. Sect. der schlesischen Gesellsch. für vaterländ. Kultur (1879) pp. 232–234.
6. Born, G.—Nachträge zu "Carpus und Tarsus." Morph. Jahrb. vol. vi. (1880) pp. 49–78.
7. Boulenger, G. A.—Catalogue of Batrachia Salientia. British Museum (1882).
8. Brandt & Ratzeburg.—Medizinische Zoologie, vol. i. Berlin (1829).
9. Breyer, F. G.—Observationes Anat. circa fabricam Ranæ pipæ. Berol (1811).
10. Brocchi, M.—Recherches sur l'ostéologie d'un Batracien Anoure provenant du Brésil (*Hemiphractus*). Ann. Sci. Nat. sér. 6 (1877), art. 7.
11. Brühl, C. B.—Zootomie aller Thierklassen. Atlas, pl. 30. Wien (1876).
12. Cope, E. D.—Sketch of the primary groups of Batrachia Salientia. Nat. Hist. Review, vol. v. (1865) pp. 97–120.
13. Cope, E. D.—On the Structure and Distribution of the Arciferous Anura. Journ. Acad. of Nat. Sci. Philadelphia, vol. vi. (1866) pp. 67–112.
14. Cope, E. D.—On the families of the Raniform Anura. Ibid. vol. vi. (1867) pp. 189–206.
15. Cuvier, G.—Recherches sur les ossemens fossiles. 4me édit. Tome x. Paris (1836), pp. 302–309. Atlas, pl. 24.
16. Dugès, A.—Recherches sur l'ostéologie et la myologie des Batraciens à leurs différens âges. Paris (1834).
17. Ecker, A.—Die Anatomie des Frosches. Part 1. Brunswick (1864).

18. Gegenbaur, C.—Untersuchungen zur vergleichd. Anatomie der Wirbelthiere. Erstes Heft. Carpus und Tarsus. Leipzig (1864).
19. Gegenbaur, C.—Critical remarks on Polydactility as Atavism (Translation). Journ. Anat. and Phys. vol. xvi. (1882) pp. 615–622.
20. Hochstetter.—Beitr. z. vergleichd. Anat. und Entwicklungsgesch. des Venensystems bei Amphibia und Fische. Morph. Jahrb. vol. xiii. (1887) pp. 117–172.
21. Hofmann, C.K.—Bronn's Klassen und Ordnungen des Thier-Reichs. Bd. vi. Amphibien. (1873–78.)
22. Howes, G. B.—Note on the Azygos Veins in the Anurous Amphibia. P. Z. S. (1888) pp. 122–126.
23. Huxley, T. H.—Article "Amphibia," Encyclopædia Britannica (9th edit.), pp. 750–771.
24. Kehrer, G.—Beiträge zur Kenntniss des Carpus und Tarsus. Bericht d. naturforsch. Gesellschaft zu Freiburg, Bd. i. Heft 4 (1886).
25. Leydig, F.—Ueber d. Bau des Zehnen bei Batrachiern u. d. Bedeutung des Fersenhöckers. Morph. Jahrb. vol. ii. (1876) pp. 165–196.
26. Leydig, F.—Die Anuren Batrachier der deutsch. Fauna. Bonn (1877).
27. Mayer, A. J. C.—Annalecten f. vergleichd. Anatomie. Bonn (1835).
28. Mayer, C.—Beiträge z. einer anatomisch. Monogr. d. *Rana pipa*. Verhandl. d. Kais. Leop.-Carol. Akad. d. Naturforsch. Bonn, Bd. xii. Heft 2 (1825), pp. 527–553.
29. Meckel, J. F.—System der vergleichend. Anatomie. II. Theil, I. Abth., Halle (1824), pp. 459–460, 487–490.
30. Mivart, St. Geo.—On the Classification of the Anurous Batrachians. P. Z. S. (1869) pp. 280–295.
31. Owen, R.—Anat. of Vertebrates, vol. i. (1866).
32. Rosenhof, A. J. Roesel von.—Historia Naturalis Ranarum nostratium. Nürmberg (1758).
33. Schultz, A. W. F.—De sceleto Bufonis palmarum. Berol (1832).
34. Van Deen.—Anat. Beschreibung einer monströsen sechsfüssigen Wasser-Frosches (*R. esculenta*). Leiden (1838).
35. Weinland, D. F.—Ueber den Beutelfrosch (*Notodelphys*). Müller's Archiv (1854), pp. 449–477.
36. Wiedersheim, R.—Lehrbuch d. vergleichd. Anatomie d. Wirbelth. Zweite Auflage. Jena (1886), pp. 204–212.
37. Walterstorff, W.—Ueber fossile Frösche insb. d. Genus *Palæobatrachus*. Part 1. Jahrb. d. naturwissensch. Vereins zu Magdeburg (1885), pp. 1–81.
38. Walterstorff, W.—Ibid. Part 2. Jahrb. (1886) pp. 83–159.

VI. EXPLANATION OF THE PLATES.

In order to facilitate comparison, all the figures are drawn in the same relative position. Each represents the dorsal surface of the left member.

Unless otherwise stated, all the preparations are represented as transparent objects. In drawing them, we have stippled ossified parts and left the cartilages clear; the effect thus obtained is more natural than that expressed in the more orthodox custom of stippling the latter.

Ligaments are indicated in black.

Plate VII.

Fig. 1. *Pipa americana*, adult ♂. Left fore foot, from above. Drawn as an opaque object. × 2½.

2. *Pipa americana*, very young specimen. Left fore foot. Ossification has not yet begun. × 30.
3. *Xenopus lævis*, adult ♀. Left hind foot. × 4.
4. *Xenopus lævis*, adult ♀. Left fore foot. Elements slightly disarticulated. × 5.
5. *Discoglossus pictus*, young specimen. Left fore foot. × 10.
6. *Discoglossus pictus*, adult ♂, 42 mm. in length. Left fore foot. All the elements are completely ossified. The white areas represent compact bone, the dark ones spongy bone. × 4.
7. *Bombinator igneus*, adult ♀, 37 mm. in length. Left fore foot. × 7.
8. *Bombinator igneus*, adult ♀, 26 mm. in length. Left hind foot. × 7.
9. *Alytes obstetricans*, tadpole, 24 mm. in length from mouth to vent. Left fore foot. × 20.
10. *Alytes obstetricans*, adult ♀, 40 mm. in length. Left hind foot. The astragalus and calcaneus and the metatarsals have alone begun to ossify. × 4.

Plate VIII.

11. *Pelodytes punctatus*, length 30 mm. Left fore foot. The hand is rotated upon the radius and ulna through more than a right angle; to facilitate comparison with the other figures, the fused radius and ulna are represented as completely disarticulated and flattened out. × 7.
12. *Pelodytes punctatus*, length 30 mm. Left hind foot. × 8.
13. *Pelodytes punctatus*, outline sketch of preaxial portion of the tarsus of the above preparation, to show the course of the ligament connecting the tarsalia of the hallux and pre-hallux. × 16.
14. *Xenophrys monticola*, young specimen, 27 mm. in length. Left fore foot. × 5.
15. *Xenophrys monticola*, enlarged drawing of the postaxial distal portion of fig. 14. The element *k* has been slightly displaced, in order to show more fully the vestigial 5th carpal. × 16.
16. *Xenophrys monticola*, adult of 40 mm. length. To show ossification of the vestigial 5th carpal. × 18.
17. *Xenophrys monticola*, length 27 mm. Left hind foot. × 12.
18. *Pelobates fuscus*, adult ♂, 54 mm. in length. Left fore foot. The fused radius and ulna have been disarticulated from the hand and laid flat; during life the radius articulates in the concavity seen at the proximal end of the lunatum (*l.*). × 7.
19. *Hyla cærulea*, adult ♀, 75 mm. in length. Left hind foot. × 3½.

19*a*. *Phyllomedusa dacnicolor*. Calcar, showing absence of the proximally directed process of its second segment. × 4.

20. *Hyla cærulea*, adult ♀, 75 mm. in length. Left fore foot. × 4½.
21. *Hyla arborea*, late tadpole. Left hind foot. Ossification has not yet begun. × 14.
22. *Pseudophryne bibronii*, ♂, 22 mm. in length. Left fore foot. × 12.

PLATE IX.

23. *Bufo calamita*, young specimen, 18 mm. in length. Left hind foot. × 12.
24. *Ceratophrys ornata*, young ♀, 140 mm. in length. Left hind foot. × 1½.
25. *Leptodactylus pentadactylus*, large ♂ specimen, 140 mm. in length. Left fore foot. Drawn as an opaque object. Nat. size.
26. *Pseudis paradoxa*, tadpole, length of tail 110 mm. Left fore foot. Ossification has not yet begun. × 6.
27. *Pseudis*, tadpole. Left hind foot. × 3½.
28. *Limnodynastes tasmaniensis*, young ♂, 38 mm. long. Left fore foot. × 6.
29. *Limnodynastes tasmaniensis*, young ♂, 38 mm. in length. Left hind foot. × 6.
30. *Phryniscus lævis*, ♀, 45 mm. in length. Left fore foot. × 5.
31. *Phryniscus lævis*, ♀, 45 mm. in length. Left hind foot. × 5.
32. *Rhombophryne testudo*, ♂, 38 mm. in length. Left fore foot. × 5.
33. *Rhombophryne testudo*, ♂, 38 mm. in length. Left hind foot. × 4½.

Reference Letters.

References marked * all apply to special allusions in the text.

FORE FOOT.—*f. i.*, foramen intercarpi. *k*, postaxial centrale. *l.*, lunatum (radiale). *n.*, naviculare (preaxial centrale). *p.*, ulnare (pyramidale). *po.* i., carpal of pollex. *po.* ii., metacarpal of pollex. *po.* iii., *po.* iv., phalanges of pollex. *po.* II., unsegmented element probably representing *po.* ii., *po.* iii., & *po.* iv. *r.*, radius. *u.*, ulna. 2, 3, 4, 5, carpals of second, third, fourth, and fifth digits. 2′, 3′, 4′, 5′, metacarpals. 4 *k*, element (*capitatum*) formed by the fusion of the carpal of the fourth digit with our postaxial centrale. 3, 4 *k*, element formed by the fusion of the third and fourth carpals with our postaxial centrale (*capitato-hamatum* of Ecker). *nk*. 1 to 4, element (*carpo-centrale*) formed by the fusion of the distal and central carpal elements. *pk*, element formed by the fusion of the ulnare with the postaxial centrale.

HIND FOOT.—*a.*, astragalus (tibiale?). *c.*, calcaneus (fibulare?). *n′.*, naviculare (centrale). *ph.* i., first segment (tarsal) of pre-hallux. *ph.* ii., second segment (metatarsal) of pre-hallux. *ph.* iii., *ph.* iv., third and fourth segments (phalanges) of pre-hallux. 1, 2, 3, tarsals of the first, second, and third digits. 2, 3, *cuboideum*, formed by fusion of second and third tarsalia. 1′, 2′, 3′, 4′, 5′, metatarsals of the first, second, third fourth, and fifth digits.

2. Descriptions of some new Species of Birds from the Island of Guadalcanar in the Solomon Archipelago, discovered by Mr. C. M. Woodford. By R. BOWDLER SHARPE, F.L.S. &c.

[Received January 18, 1888.]

The Accipitres brought by Mr. Woodford from Guadalcanar are extremely interesting, and no less than three new species of *Astur* are represented in his collection.

I propose to call them :—

ASTUR HOLOMELAS, sp. n.

Adult male. Entirely black, with a slaty-grey gloss on the back, rump, wings, and tail, and decidedly more slaty on the under surface of the body : " bill slaty black ; cere and orbital skin yellow ; iris